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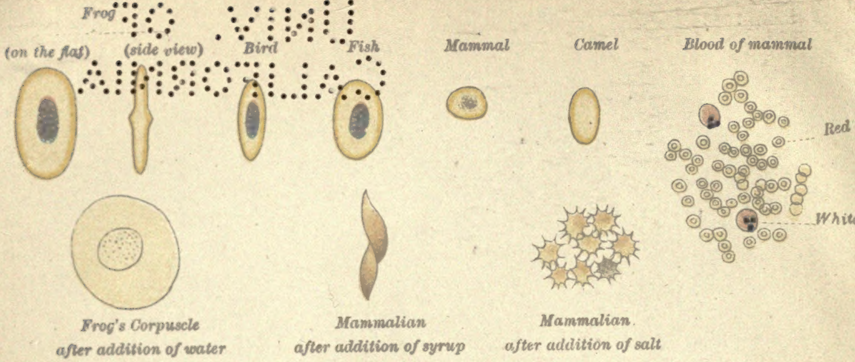
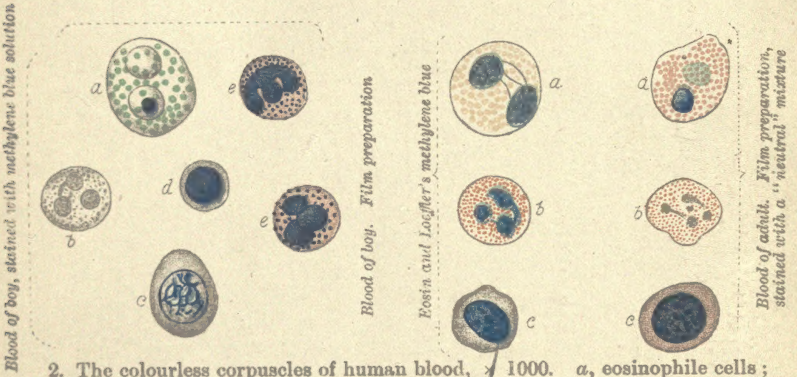
A MANUAL OF VETERINARY PHYSIOLOGY

UNIV. OF
CALIFORNIA

PLATE I.

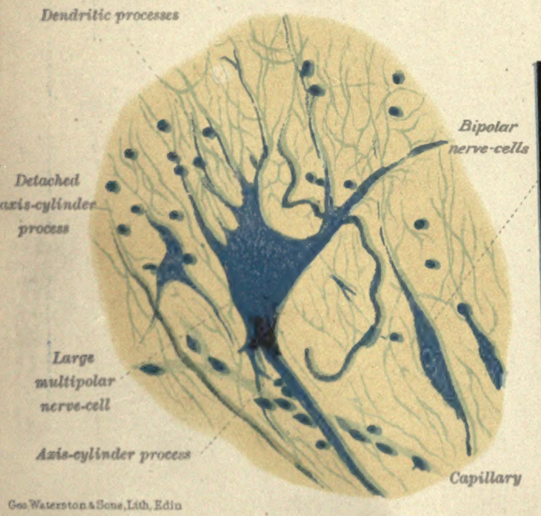

Frog
(on the flat)
(side view)
Bird
Fish
Mammal
Camel
Blood of mammal
Red
Whit
Frog's Corpuscle after addition of water
Mammalian after addition of syrup
Mammalian after addition of salt

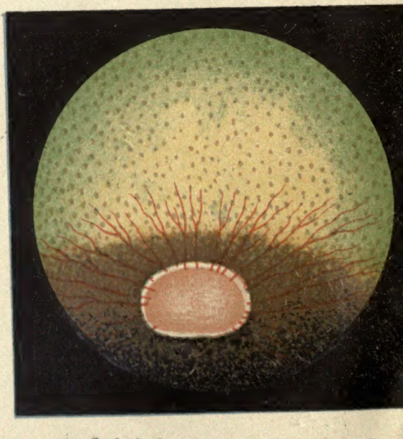
1. Red blood-corpuscles.


Blood of boy, stained with methylene blue solution
a
e
b
d
e
c
Blood of boy. Film preparation
Eosin and Loeffler's methylene blue
a
b
c
a
b
c
Blood of adult. Film preparation, stained with a "neutral" mixture

2. The colourless corpuscles of human blood, × 1000. *a*, eosinophile cells; *b*, finely granular oxyphile cells; *c*, hyaline cells; *d*, lymphocyte; *e*, polymorphonuclear neutrophile cells (Kanthack and Hardy). The magnification is much greater than in 1.

3. Cover-glass preparation of spinal cord of ox, × 250. (*Stained with methylene blue*).


Dendritic processes
Detached
axis-cylinder
process
Bipolar
nerve-cells
Large
multipolar
nerve-cell
Axis-cylinder process
Capillary



4. Ophthalmoscopic view of fundus of the horse.

Geo Waterston & Sons, Lith, Edin

A MANUAL
OF
VETERINARY PHYSIOLOGY

BY

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FOURTH EDITION

LONDON
BAILLIÈRE, TINDALL AND COX
8 HENRIETTA STREET, COVENT GARDEN
1912

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TO THE MEMORY OF

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LATE PROFESSOR OF PHYSIOLOGY IN THE
UNIVERSITY OF CAMBRIDGE

255238

PREFACE TO THE FOURTH EDITION

It is nearly twenty years since the first edition of this work was published. In consequence of a fourth edition being called for, an endeavour has been made to deal with the subject on a somewhat wider basis than previously, and this has necessitated the book being rewritten and enlarged.

The work is essentially a veterinary, and not a comparative, physiology. It treats of physiology not only from its theoretical aspect, but from the point of view of clinical utility. The requirements of the student and practitioner have consequently not been lost sight of, and every opportunity has been taken in the text to point out the clinical application of physiological facts. To several chapters a special appendix is added, in order to enforce the lesson that pathology is only physiology out of health.

As in the last editions, so also in this, I have derived much help from the well-known English Textbooks on Human Physiology, and wish to express my special indebtedness to the similar works of Professor Howell of Baltimore, and Professor Stewart of Cleveland.

The authorities and observers whose work has assisted in the preparation of various chapters are acknowledged in the text, or included in the list of authorities to be found at the end of the volume.

Numerous references have been made to the monumental *Traité de Physiologie Comparée des Animaux*, by the late Professor G. Colin, of the Veterinary School of Paris. He was the father of veterinary physiology, and though his treatise was published over forty years ago, his experimental work will last for all time.

For permission to utilise figures I have to thank the editors of the *Quarterly Journal of Experimental Physiology*, Professor Stewart of Cleveland, and Professor S. Sisson of the Ohio State University, in addition to those acknowledged in former editions.

My friend, Dr. Sheridan Lea, F.R.S., has again been good enough to undertake the laborious work of reading all the proofs. His acute critical faculty has been invaluable, and I tender him my warmest thanks.

F. S.

LONDON,
February, 1912.

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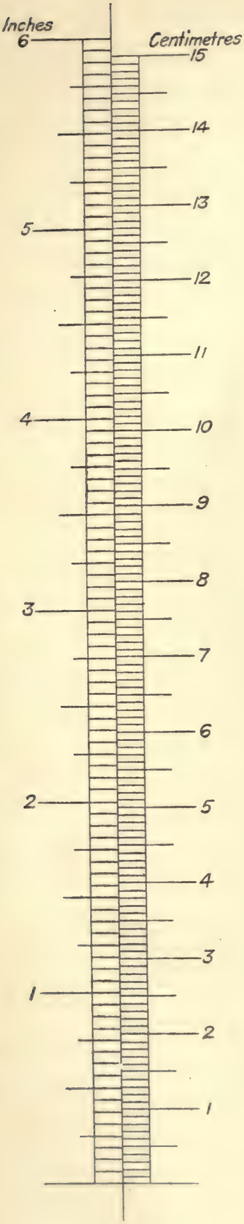
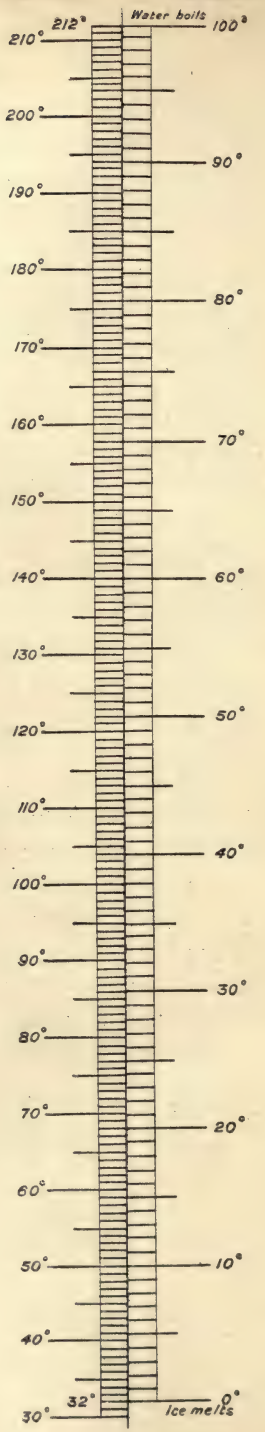

Inches
Centimetres


Fahrenheit.
Centigrade.
Water boils
212°
100°
210°
200°
90°
190°
180°
80°
170°
160°
70°
150°
140°
60°
130°
120°
50°
110°
40°
100°
90°
30°
80°
70°
20°
60°
50°
10°
40°
32°
0°
Ice melts
30°

A COMPARISON OF SOME BRITISH AND METRIC UNITS

Degrees Fahrenheit = $\frac{9}{5}$ C.° + 32.
Degrees Centigrade = $\frac{5}{9}$ (F.° − 32).

Length
1 inch = 25·4 millimetres = 2·54 centimetres.
1 foot = 304·8 ,, = 30·48 ,,
1 yard - - = 91·44 ,,
1 mile = 1609·3 metres = 1·609 kilometres.
5 miles - - = 8 kilometres (nearly)

1 metre = 1,000 millimetres = 39·37 inches.
1 centimetre = $\frac{1}{100}$ metre = 0·39 inch.
1 kilometre = 1,000 metres = 0·62 mile.

To convert millimetres into inches, × ·039. Converse, × 25·4.
To convert metres into yards, × 1·09. Converse, × ·914.

Weight
1 grain = 0·064 gramme = 64·8 milligrammes.
1 ounce (avoir.) = 28·35 grammes = 457·5 grains.
1 pound ,, = 453·60 ,, = $\frac{1}{2}$ kilogramme (approx.).
1 cwt. - - - - = 50·8 kilogrammes.
1 ton - - - - = 1,016 ,,

1 kilogramme = 1,000 grammes = 2·2 pounds (avoir.).
1 gramme - - - = 15·432 grains.
1 milligramme = $\frac{1}{1000}$ gramme = 0·0154 grain = $\frac{1}{65}$ grain (nearly).

To convert grammes into ounces, × 0·0352. Converse, × 28·35.
To convert kilogrammes into pounds, × 2·2. Converse, × 0·454.

Capacity
1 fluid ounce = 28·4 cubic centimetres.
1 pint = 568·0 ,, ,,
1 gallon = 4·54 litres.
1 peck = 9·08 ,,
1 bushel = 36·32 ,,
1 cubic inch = 16·38 cubic centimetres.
,, foot = 28·33 litres.

1 litre = 1,000 cubic centimetres = 1·76 pints (imperial) = 61 cubic inches.
1 cubic centimetre = 0·061 cubic inch = 1 gramme of distilled water at its greatest density.
1 cubic metre = 1,000 litres = 35·3 cubic feet.

To convert litres into pints, × 1·76. Converse, × ·568.
To convert litres into gallons, × 0·22. Converse, × 4·543.
To convert litres into cubic feet, × 0·03532. Converse, × 28·33.

Work
1 foot-pound = 0·138 kilogramme-metre.
1 foot-ton = 309·12 kilogramme-metres.
1 kilogramme-metre = 7·25 foot-pounds.

1 unit of heat (British) = heat necessary to raise 1 pound of water through 1° F.
1 calorie (Metric) = heat necessary to raise 1 gramme of water through 1° C.
Mechanical equivalent of heat-unit = 772 foot-pounds.
,, ,, calorie = 424 gramme-metres.
,, ,, kilo-calorie = 424 kilogramme-metres.

CORRIGENDA

Page 21, line 21 from bottom, *for* 'luconuclein' *read* 'leuconuclein.'
,, 30, ,, 15 ,, top, after Fig. 12 insert 'or better still Fig. 45.'
,, 48, ,, 19 ,, bottom, *for* 'Remark' *read* 'Remak.'
,, 49, ,, 2 ,, top, *for* '12' *read* '31.'
,, 52 ,, 11 ,, top, *for* 'happen' *read* 'happens.'
,, 56, ,, 14 ,, bottom, *for* 'heart' *read* 'heart-beat.'
,, 151, line 14 ,, bottom, *for* 'has been' *read* 'is.'
,, 163, ,, 8 ,, bottom, *for* 'proteid' *read* 'protein.'
,, 174, ,, 7 ,, bottom, *for* 'Ellenberg' *read* 'Ellenberger.'
,, 190, ,, 6 ,, top, *for* 'peptoids' *read* 'peptids.'
,, 223, in explanation to Fig. 78, *for* 'is' *read* 'are.'
,, 296, line 12 from top, *for* 'proteid' *read* 'protein.'
,, 323, ,, 3 ,, top, *for* 'much' *read* 'plentiful.'
,, 326, ,, 12 ,, bottom, *for* 'urolytic' *read* 'uricolytic.'
,, 330, ,, 3 ,, bottom, *for* 'which' *read* 'and.'
,, 354, ,, 21 ,, bottom, *for* 'metabolism' *read* 'equilibrium.'
,, 377, ,, 3 ,, top, *for* 'optic thalamus' *read* 'corpus striatum.'
,, 487, ,, 9 ,, top, *for* 'are' *read* 'is.'
,, 536, ,, 10 ,, top, *for* 'miosis' *read* 'myosis.'
,, ,, ,, 11 ,, top, *for* 'miotics' *read* 'myotics.'
,, 577-580, *passim*, *for* 'tympanum' *read* 'membrana tympani.'

Note to p. 458. The term 'colliculi' is now coming into use to denote the *corpora quadrigemina*. Its shortness is convenient, and it avoids confusion in the case of reptiles, birds, fish, etc., where these structures are bigeminate.

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A MANUAL OF VETERINARY PHYSIOLOGY

CHAPTER I

THE BLOOD

THE special functions of the blood are to nourish all the tissues of the body, and thus aid in their growth and repair ; to furnish material for the purpose of the body secretions, to supply the organism with oxygen, without which life is impossible, and finally to convey from the tissues the products of their activity. To enable all this to be carried out the blood is constantly in circulation, is rapidly renewed, is instantaneously purified in the lungs, and, by means of certain channels, is placed directly in communication with the nourishing fluid absorbed from the intestines, by which it is constantly repaired.

Physical Characters.—Blood is a red, opaque, rather viscous fluid, the tint of which depends upon whether it is drawn from an artery or a vein ; in the former it is of a bright scarlet colour, whilst in the latter it is of a purplish red. The colour is due to a pigment called hæmoglobin contained in the red corpuscles. Whether the colour is scarlet, as in blood from an artery, or purplish, as from a vein, depends on the difference in the amount of oxygen with which the hæmoglobin is combined.

Owing to the **reaction** given by blood to ordinary test-papers, the fluid has hitherto been described as alkaline in reaction. New methods in physical chemistry * have, however, shown that blood possesses little more alkalinity than distilled water, and may for practical purposes be regarded as neutral.

Sodium carbonate, which exists largely in blood and was believed to confer alkalinity on this fluid, is now known to form bicarbonate with the carbonic acid present, and this yields no alkalinity on dissociation. The apparently alkaline reaction obtained with litmus is not a true reaction, but due to the litmus acid driving out the sodium from the weaker carbonic acid.

---

* The reaction of a solution is determined by the proportion of hydrogen and hydroxyl ions. If hydrogen ions are in excess, the fluid is acid ; if hydroxyl ions predominate, an alkaline reaction exists.

Excepting in the herbivora, considerable amounts of acid may be administered by the mouth or formed in the tissues without affecting the neutral reaction of the blood, the acid being neutralised by the ammonia split off from proteins. Proteins may, in fact, act in a dual capacity, either as bases neutralising acidity, or as acids neutralising alkalinity.

The carbon dioxide of the blood is in the main united with bases, especially soda, and the total carbonic acid content of a sample of blood is a measure not only of its capacity for carrying carbonic acid, but also for maintaining the neutral reaction of the blood. With the herbivora the carbonic acid content is readily reduced under the influence of acids administered by the mouth or formed in the body, and this protective mechanism is thus reduced.

The recently-drawn blood of the cat and dog has a peculiar and decidedly disagreeable smell ; this is not observed in the blood of the horse and ox. The taste of blood is saltish, due to the amount of sodium chloride it contains.

The **specific gravity** varies in different animals : in the horse, ox, and pig, 1060 ; sheep, 1050-1058 ; dog, 1050 (Colin). According to Hoppe-Seyler, the specific gravity of the liquor sanguinis of the horse is 1027 to 1028, and the specific gravity of the cells 1105. This considerable difference between the specific gravity of the cells and the liquor sanguinis in the horse accounts for the rapid manner in which the cells sink in horse's blood when drawn from the body, producing during the process of clotting the so-called ' buffy coat.'

Composition of the Blood.—Blood consists of a fluid portion or plasma in which the blood cells or corpuscles are suspended.

Plasma, or **liquor sanguinis**, is a yellow-coloured, somewhat viscid, fluid, containing in solution—

Protein.
Extractives.
Mineral matter.
Enzymes.
Unknown substances (*i.e.*, immune bodies). (See p. 8.)

The corpuscles are—

Red corpuscles, or erythrocytes.
White corpuscles, or leucocytes.
Platelets.

So far as the presence of the various constituents is concerned, the blood of any one animal presents a very uniform character, but their amount in the blood of different animals is liable to great variation. The composition of the blood is also affected by the source from which it is derived; the blood from an artery does not exactly represent that from a vein.

Plasma forms about 66 per cent. of the blood, and consists of three proteins, which are held in solution—viz., *fibrinogen, paraglobulin (serum-globulin)*, and *serum-albumin*. The two former belong to the globulin group of proteins; the latter to the albuminous group, of which egg-albumin is typical.

The three proteins may be separated by the employment of certain neutral salts. **Serum-albumin** is precipitated by saturation with ammonium sulphate. Its solution in a neutral or acid medium is thrown down by heat. The temperatures of coagulation, 70° to 75° C. (158° to 167° F.), would appear to indicate that there are two or three different proteins classed as serum-albumin.

This substance is found not only in blood plasma, but in lymph. It also forms a part of such secretions as milk. Its source is believed to be the protein substances of the food which are taken up from the intestinal canal, though there is no experimental proof of the correctness of this view. Serum-albumin obtained from the blood of the horse may readily be made to crystallise.

Paraglobulin or **serum-globulin** is distinguished by being precipitated by saturation with magnesium sulphate, or half saturation with ammonium sulphate. In neutral or faintly acid solutions it is coagulated by heating to 75° C. (167 F.), and there is reason to think from the behaviour under analysis of the paraglobulin obtained from serum that this substance is probably a mixture of two or three allied proteins. It is supposed that the source of paraglobulin is twofold—first from the protein substances of the food; and secondly from the disintegration of the white cells of the blood; but in both cases proof is wanting.

Fibrinogen constitutes but a small proportion of the total protein of plasma. It is precipitated from solution by half saturation with sodium chloride. It belongs to the group of proteins known as globulins, and is a substance of remarkable interest, for on its conversion from a fluid to a solid condition depends the phenomenon of the coagulation of the blood. Like the other proteins in plasma, it coagulates on heating, but at a much lower temperature, for fibrinogen is coagulated at 56° to 60° C. (133° to 140° F.). Blood so treated is no longer capable of clotting, owing to its fibrinogen being coagulated. The source of fibrinogen in the body is unknown; it is supposed to be connected with the destruction of leucocytes, and there is also some evidence of the liver being concerned in its formation.

Perhaps the nearest approach to pure plasma is the fluid found in the pericardial and abdominal cavities. That which is effused into the chest during an attack of pleurisy is plasma to start with, but if it has undergone coagulation and fibrin (false membranes) has been formed, then the resulting fluid is serum.

In the following table is shown the composition of the blood plasma of different animals. The figures are expressed as grammes in 100 c.c. of blood. It will be observed that in the horse the globulins exceed the albumins, while in the dog and pig the reverse holds good. The poverty of dog's blood in total proteins, as compared with that of the horse and pig, is also striking.

	Total Proteins.	Serum-Albumin.	Para-globulin.	Fibrinogen.
Dog - - - -	6·03	3·17	2·26	0·60
Sheep - - - -	7·29	3·83	3·00	0·46
Horse - - - -	8·04	2·80	4·79	0·45
Pig - - - -	8·05	4·42	2·98	0·65

So long as the blood is in circulation or prevented from clotting, its fluid portion is termed 'plasma'; but if blood be allowed to coagulate, in course of time it separates into a solid clot and a liquid portion, and this liquid is no longer known as plasma, but as serum. Serum is therefore plasma which is modified as the result of coagulation, and as this latter process is attended by the production of fibrin, it may be said that serum is plasma minus the fibrin-forming elements.

Serum does not contain fibrinogen, for the reason that the latter has been used up in the process of clotting, but it possesses, in addition to serum-albumin and paraglobulin, a body known as *fibrino-globulin*, believed to be split off from fibrinogen in the act of clotting, and *nucleo-protein*, supposed to be derived from the fibrin ferment; some observers doubt the existence of this latter substance in the serum. The total protein content of serum is 8 or 9 per cent., and so resembles the protein content of plasma; the extractives and salts are the same in both fluids.

In the following table a comparison is made between the proteins of plasma and serum:

Plasma.	Serum.
Serum-albumin.	Serum-albumin.
Paraglobulin.	Paraglobulin.
Fibrinogen.	Fibrino-globulin.
	Nucleo-protein.

Corpuscles.—Blood examined under the microscope is found to consist of an enormous number of bodies termed 'corpuscles,' floating in the liquor sanguinis. These corpuscles are of two kinds, red and white; the former are the more numerous, the latter are the larger.

The **Red Corpuscles** constitute 33 per cent., or one-third of the total blood. Viewed under the microscope, they are found to be biconcave discs, circular in shape, and possessing no nucleus (Plate I.) ; they are soft, flexible, elastic bodies, capable of having their shape readily altered by pressure, which enables them to pass along the finest capillaries. The colour of a single corpuscle is yellow, but when heaped together they appear red, and thus give the colour to the blood.

In all mammals, excepting the camel tribe, the red cells are circular and biconcave ; in the Camelidæ they are elliptical and biconvex. In all vertebrates below mammals they are biconvex, oval, and nucleated (Plate I.). The corpuscles vary in size in different animals, being smallest in the deer tribe and largest in the elephant, as may be seen in the diagram (Fig. 1). When a drop of blood is shed, the red cells at first move quite freely each over the other. In a short time they tend apparently to become sticky, and when this state is reached they have a tendency to lie in long rows, with their flat surfaces in close contact, resembling the appearance of a pile of pennies. This condition is not marked in horses' blood.

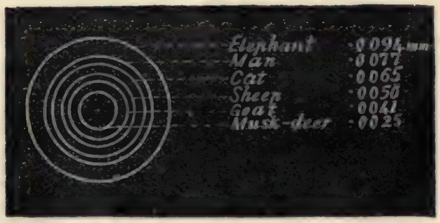

Fig. 1.—Diagram showing Relative Size of Red Corpuscles of Various Animals (Stewart).

A red blood-cell is composed of a spongy stroma, holding in its meshes the red colouring matter. The stroma or framework of the corpuscle consists of nucleo-albumin, lecithin, cholesterin, and salts ; the red colouring matter, hæmoglobin, forms no less than 32 per cent. of the total solid matter of the fresh corpuscle.

Great discussion has taken place as to whether the corpuscle is a perforated mass of protoplasm containing no covering, or whether it possesses a cell-wall, as its microscopical appearance indicates. At present the general feeling is that there is no cell-wall, but that there is a condensation of the cell-substance at the periphery, while within the spongy substance of the interior is lodged the hæmoglobin, probably in an amorphous condition, certainly not in a crystalline state, and perhaps not in solution. It is further supposed that the large amount of lecithin and cholesterin present in the stroma gives permeability to the external layer of the cell. For example, water, alcohol, ether, and a solution of urea can pass in, but not neutral salts.

The number of corpuscles in the blood is determined approximately either by the method of Gowers or Malassez. The principle on which these methods are based is the same—a known quantity of blood is diluted with a known bulk of artificial serum and thoroughly mixed; of this a small drop is placed in a counting-chamber of known capacity, which is ruled into squares, and examined under the microscope. The blood-cells occupying the squares are counted, as may readily be done, and the mean of them taken. In the horse the mean number of red blood-corpuscles per cubic millimetre is 7,212,500, and in the ox 5,073,000. Taking the amount of blood in the horse as 29 litres (50 pints, or 66 pounds), this gives 204,113,750,000,000 as the approximate number of red cells in the body (Ellenberger).* It is evident that a loss of water from the blood means a larger relative proportion of red cells present, while an excess of water, by diluting the blood, would show a loss of red cells; thus the number of the red cells is increased by sweating, by the excretion of water from the bowels and kidneys, and by starvation, while it is diminished by pregnancy and copious draughts of water. But apart from these conditions, it is undoubted that an actual increase or decrease in the number of red cells may occur, this numerical variation being especially marked in some diseases. The shape of the red cell is affected by the amount of fluid in the plasma; if the latter be artificially concentrated, water diffuses from the corpuscle to the plasma, and in consequence it shrinks and becomes wrinkled (Plate I.). If the plasma be diluted, the red cells swell. A 0·9 per cent. solution of sodium chloride causes the corpuscles neither to shrink nor swell; this strength is known as 'physiological salt solution,' and may be employed for the purpose of transfusion.

Each red cell offers a certain absorbing surface for oxygen, which, if calculated on the total number of corpuscles, is something enormous, being equal for the horse to a square having a side of 164 metres (180 yards). The opacity of blood is due to the red cells reflecting light as the result of their peculiar shape; if the cells be destroyed, the blood becomes transparent or, as it is termed, 'laky,' of which more will presently be said.

The greater part of the red cell consists, as already stated, of hæmoglobin, a substance possessing a remarkable affinity for oxygen; this it obtains at the lungs, and leaves behind in the tissues. The hæmoglobin of the red cells, therefore, exists in two states, one in which it is charged with oxygen called 'oxy-hæmoglobin,' and the other in which it has lost its oxygen and is known as 'reduced hæmoglobin.' The process of oxidation in the lungs and reduction in the tissues is constantly occurring at every cycle of the circulation, with the ultimate result that the red blood-disc, the life of which is probably only a matter of a few days, gets worn out and dies. In this condition it is cast off from the system, being got rid of through the medium of the liver. In addition to the blood-stream, other suggested seats of destruction are the spleen, bone-marrow, and lymph-glands, but no definite statement can at present be made. When the red cells die, their hæmoglobin is set free, and decomposed into an iron-free residue from which, probably, all the pigments of the body are formed, certainly those of the bile.

---

* 'Physiologie der Haussäugethiere.'

The seat of formation of the red cells is in the red marrow of bones, where they are formed from certain nucleated colourless cells ; there are several varieties of blood-forming cells (*erythroblasts*) in the red marrow, and it is not definitely settled which of these furnish the red blood-cells. All other seats of formation are doubtful. In the embryo the future red cells for a certain period are nucleated and contain no hæmoglobin, but these are gradually replaced by non-nucleated, hæmoglobin-holding corpuscles before birth. It is interesting to observe that both in the embryo and in the adult the red cells are derived from a nucleated precursor.

By the time the corpuscle takes its place in the blood as a cell which has lost its nucleus it is on the downward path. This and other considerations have assigned its probable life in the blood-stream as only a matter of a few days.

Hæmolysis.—It has been pointed out that in a normal condition the hæmoglobin is contained wholly within the red cells, and that there is no passage of colouring matter from the cells to the fluid in which they are carried. Anything which kills the red cell, or, if we adopt the cell-wall view, anything which kills the envelope, allows the hæmoglobin to escape.

The cells may be destroyed by alternately freezing and thawing the blood, or by the passage through it of electric shocks, or by the addition of certain agents such as chloroform, ether, bile salts, tannic or boric acids, etc. The hæmoglobin becomes liberated from the broken-up cells, and stains the naturally yellow plasma a red colour. The blood under these circumstances, as we have seen, is no longer opaque, but transparent, and the term 'laky' well describes its colour. The entire process is described as 'hæmolysis.'

Most of the above causes of hæmolysis act as protoplasmic poisons ; they kill the cell, and as the osmotic pressure of the plasma is slightly less than that of the corpuscular contents, the hæmoglobin diffuses out. Poisons such as ether and chloroform are probably hæmolytic owing to their chemical effect in dissolving the cholesterin and lecithin of the corpuscles. Others may unite with these substances and render them soluble, by which means hæmoglobin escapes from the cell. Snake venom and the poison of bees and of certain spiders produce hæmolysis, so also some pathological toxins, of which the most noteworthy in the horse is that producing so-called *azoturia*. The most remarkable result is that obtained by adding to, or injecting into, the blood of one animal the serum of an animal of a different species. This leads in certain cases to destruction of the red cells, and a chain of results of the highest practical importance. If, for example, the fresh serum of the blood of the dog be added to the washed red corpuscles of the rabbit, the latter are destroyed and the colouring matter liberated. If the serum of the dog be previously heated to 55° C. (132° F.), it may be added in any quantity to the washed blood-cells of the rabbit, without producing any effect on them; evidently something has been destroyed by the process of raising the temperature. This something can be restored by adding to the heated dog's serum some serum which is not hæmolytic for rabbit's cells (say rabbit serum). The effect now is to render the dog's serum once more hæmolytic.

So far the phenomenon is physiological. The serum of any animal, however, can be rendered hæmolytic for the corpuscles of another species by injecting the first with the red corpuscles of the second. If, for example, the corpuscles of species A, say an ox, be injected into species B, say a goat, the serum of the goat becomes actively hæmolytic for the corpuscles of the ox, and will cause hæmoglobinuria and death when inoculated to the latter animal. The goat's serum will also hæmolyse the corpuscles of the ox *in vitro*. If it be heated to 55° C., however, it loses its hæmolytic action, which can be restored to it in the way mentioned above. The explanation is that there are two substances in the hæmolytic serum concerned in the production of hæmolysis. One is relatively unstable, and is destroyed by a temperature of 55° C. This is the destroying agent, which is known as the *complement*. The other substance is spoken of as the *immune body*, the *anti-body*, the *amboceptor*, or *substance sensibilisatrice*. It is not destroyed by a temperature below 65° C. When a hæmolytic serum is heated to 55° C. for half an hour, its hæmolytic action is lost, because the complement has been destroyed. It can be restored by adding fresh, though non-hæmolytic, serum from another animal—a guinea-pig, for example—because the complement is not specific, and is the same in all animals. If a hæmolytic serum be heated before injection to the animal, it still causes hæmolysis, because the complement is supplied by the animal's serum. The immune body, on the other hand, is specific for the corpuscles of the species against which it has been prepared, and for those of no other. These phenomena are closely related to the reaction of the body towards bacteria, and are concerned in the production of antitoxins.

Agglutination is the process by which the red blood-corpuscles are collected together in clumps, under the influence of an agent in the blood known as an *agglutinin*. Agglutination frequently precedes hæmolysis, but it is independent of it, for if the *complement* of a hæmolytic serum be destroyed by heating to 55° C., the agglutinating substance remains, being relatively unaffected by heat.

If an animal, say a rabbit, be injected with the blood-cells of the dog, the serum of the rabbit, which normally has no effect on the blood-cells of this animal, becomes powerfully hæmolytic for dog's corpuscles, and, further, it agglutinates for the corpuscles of the dog. An agglutinin has, therefore, been experimentally produced in the serum of the rabbit. The phenomenon of agglutination is employed in bacteriology as an important aid to diagnosis.

Precipitins.—If the serum of one animal be injected into another of a different species, it is found that the serum of the receiver is capable of causing a precipitate in the normal serum of the donor ; for example, if a rabbit be injected with the serum of a dog, the rabbit serum will in course of time produce a precipitate if added to dog's serum, but not if added to the serum of any other animal. Such substances are known as *precipitins*, and are employed for the purpose of identifying different bloods and for other purposes. They may, for example, be used for the determination of the flesh of different animals—horse-flesh, for instance, when sold as beef; for if a rabbit be injected with an extract of horse-flesh, its serum will produce a precipitate with extracts of horse-flesh, but not ox-flesh.

Blood Platelets.—These may be seen in the circulating blood, but more easily in blood which has been shed—certain small colourless cells one quarter the size of a red corpuscle, and usually of a round or oval shape. In shed blood they agglutinate and rapidly disintegrate, but under suitable conditions they may be kept alive, when they exhibit amœboid movements. At one time they were regarded as disintegration products of the red cells, but this view is no longer held, and it is probable they are distinct cellular elements. Of their function little or nothing is known, but that they play an important part in blood-clotting is undoubted.

Hæmoglobin is the red colouring matter of the blood, and is remarkable for being one of the most complex substances in organic chemistry. It contains the elements C, H, O, N, S, and Fe. The molecule of hæmoglobin is probably the largest of any known substance which is capable of being crystallised. If, as is most usually assumed, its molecule contains one atom of iron, then, on this assumption, and from a knowledge of its percentage composition, the molecular formula for the hæmoglobin of horse-blood may be represented as $C_{112}H_{1130}N_{214}S_2FeO_{245}$, which is some 5,000 times that of a molecule of hydrogen. It has been supposed that the size of the hæmoglobin molecule is connected with the heavy atom of iron which it has to support. The function of the iron is closely connected with the power the pigment has of combining with oxygen.

Hæmoglobin is a protein, but is distinguished from the majority of the other members of its class by the comparative ease with which it may be obtained in a crystalline form ; while, on the other hand, its behaviour in a dialyser is not that of a crystalloid, but a colloid.

Hæmoglobin, under the influence of heat, acids, or alkalies, is broken up in the presence of oxygen into a simple protein, *globin,* and a pigment, *hæmatin :* it is therefore a compound of a protein body with hæmatin ; the protein portion of the molecule represents the greater part, the pigment being only 4 per cent. of the total. In the protein portion is found all the sulphur, and in the pigment all the iron of the molecule. The pigment hæmatin exists in the living blood as hæmoglobin, the great difference between these two substances being that hæmatin forms a firm while hæmoglobin forms a feeble combination with oxygen.

The union of oxygen with hæmoglobin is a true chemical compound, a definite weight of hæmoglobin uniting with a fixed volume of the gas, and forming **oxyhæmoglobin.** This is not a stable compound ; it readily gives off its oxygen either in the presence of oxidisable substances, or in an atmosphere free from oxygen, and by so doing becomes **reduced hæmoglobin.** It is oxyhæmoglobin which gives the bright colour to arterial blood, and it is the presence of partly reduced hæmoglobin which gives the darker tint to venous blood. The change in colour which venous blood undergoes on exposure to the air is due to the absorption of oxygen by hæmoglobin. Similarly the blood is charged with oxygen in the lungs, brought back to the heart, and distributed all over the body to the tissues ; here it gives up the bulk of its oxygen, and as partially reduced hæmoglobin is brought back by the veins to the heart for distribution to the lungs, where it renews its oxidised condition. Excepting in the latest stages of asphyxia, hæmoglobin is never completely reduced in the body.

Oxygen is not the only gas with which hæmoglobin is capable of forming a chemical compound. Carbon monoxide unites with it, forming the definite compound **carbonic oxide hæmoglobin.** In great contrast to oxyhæmoglobin, this is a remarkably stable compound, the carbon monoxide holding so tenaciously to hæmoglobin that oxygen cannot displace it. This explains the highly poisonous nature of this gas. The spectrum of CO hæmoglobin closely resembles that of oxyhæmoglobin (see Fig. 2). A still more poisonous compound is **nitric oxide hæmoglobin,** since this gas is attached to the hæmoglobin even more tenaciously than carbon monoxide.

Hæmoglobin also forms a compound with carbon dioxide, producing **carbohæmoglobin** ; this compound may be formed even when the hæmoglobin is already nearly saturated with oxygen, and the explanation which has been offered is that while the oxygen is united to the pigment portion of the molecule, the carbon dioxide is united to the protein portion.

When examined spectroscopically, oxy- and reduced hæmoglobin produce quite distinctive spectra, by which they may be readily recognised. To state the matter broadly, oxyhæmoglobin gives two well-marked dark absorption bands or shadows in the green portion of the spectrum, one band being wide, the other narrow, while reduced hæmoglobin gives one wide single band in nearly the same position (Fig. 2). The change from oxyhæmoglobin to reduced hæmoglobin may readily be brought about in spectroscopic examination by the addition of an alkaline solution of ferrous tartrate (Stokes's fluid) to the blood.

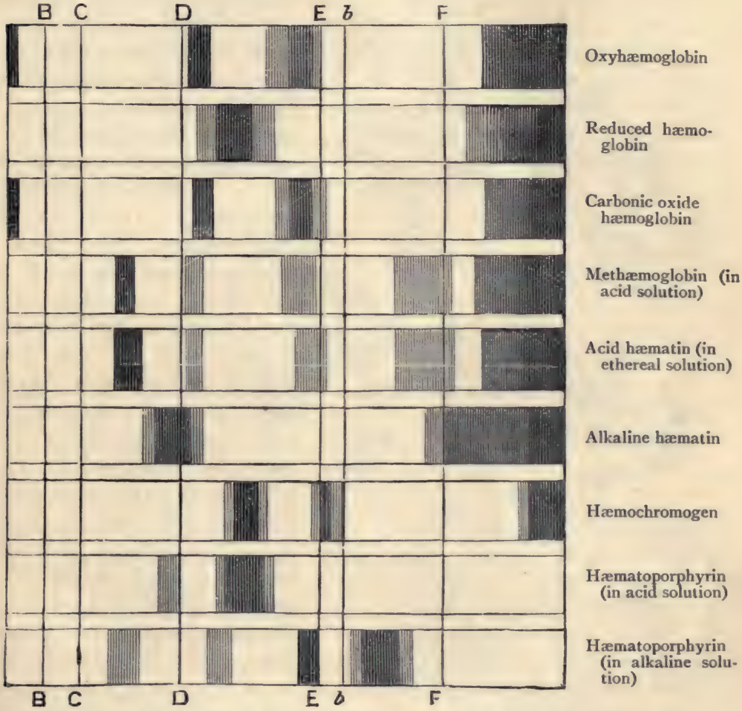
B
C
D
E
b
F
Oxyhæmoglobin
Reduced hæmoglobin
Carbonic oxide hæmoglobin
Methæmoglobin (in acid solution)
Acid hæmatin (in ethereal solution)
Alkaline hæmatin
Hæmochromogen
Hæmatoporphyrin (in acid solution)
Hæmatoporphyrin (in alkaline solution)
B
C
D
E
b
F

Fig. 2.—Table of Spectra of Hæmoglobin and its Derivatives (Stewart).

Crystals of hæmoglobin, when seen in bulk, are of a dark red or bluish-red colour ; they are extremely soluble in water, the solution being dichroic—viz., green by reflected and bluish-red by transmitted light. The blood of the horse, cat, dog, and guinea-pig readily yields crystals of oxyhæmoglobin ; that of the ox, sheep, and pig crystallises with difficulty. The crystals are generally rhombic prisms or needles, but the form differs according to the animal (Fig. 3). Reduced hæmoglobin can only be crystallised with great difficulty, and in an atmosphere free from oxygen

The total amount of hæmoglobin in a horse's body is about 4 kilogrammes (8·8 pounds), and the amount of iron contained in this is about 17 grammes (257 grains). This calculation is based on the assumption that the amount of blood in the body is 29 litres (50 pints).

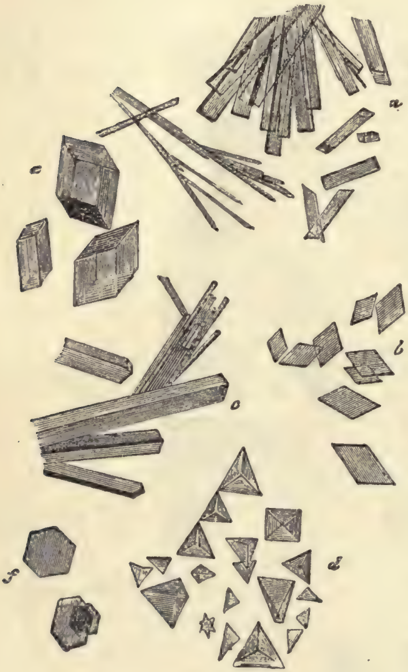

FIG. 3.—OXYHÆMOGLOBIN CRYSTALS.

a, *b*, From man ; *c*, from cat ; *d*, from guinea-pig ; *e*, from hamster ; *f*, from squirrel (Frey).

In the dried red blood-cells hæmoglobin exists in the proportion of 90 to 94 per cent., in the corpuscle under normal conditions it represents 32 per cent. of its weight ; while in the total blood of the horse it forms 13·15 per cent., in the ox 9·96 per cent., sheep 10·34 per cent., pig 12·7 per cent., and dog 9·77 per cent. (Ellenberger).[*] The younger the animal the less hæmoglobin ; males have more than females, and castrated animals more than entires (G. Müller).[†]

Methæmoglobin is a derivative of hæmoglobin, and may be produced by allowing blood to be exposed to the air until it becomes brown in colour and acid in reaction ; or it may be prepared by the action of acids or alkalies on oxyhæmoglobin. This substance contains the same amount of oxygen as hæmoglobin, but it will not part with it, excepting in the presence of reducing agents ; for respiratory purposes it is therefore useless. It is not a normal constituent of the blood, but may be found in the urine whenever a sudden breaking-down of red corpuscles occurs, as, for example, in the so-called azoturia of the horse. Its spectrum is seen in Fig. 2.

[*] 'Physiologie der Haussäugethiere.'

[†] *Ibid.*

Hæmatin, as one of the decomposition products of hæmoglobin, has been previously referred to. It will be remembered that it is obtained by decomposing hæmoglobin by boiling, or the addition of alkalies, acids, or acid salts ; in either case the hæmoglobin splits up into a substance containing the iron, known as **hæmatin**, and a proteid substance or substances termed **globin.** Hæmatin in the dry state strongly resembles iodine in appearance ; it has a metallic lustre, a blue-black colour, is not crystallisable, and yields, when pulverised, a dark brown powder, which contains 8·82 per cent. of iron. It is a remarkably stable substance, and the colouring matter presents a distinctive spectrum both in an acid and alkaline solution (see Fig. 2). Alkaline solutions of hæmatin can take up and give off oxygen as does hæmoglobin. When hæmatin is treated with glacial acetic acid and common salt, it yields **hæmin**, which, when examined microscopically, is found to consist of prismatic crystals, dark or nearly black in colour (see Fig. 4). Hæmin crystals may be readily produced by warming the dried blood with a drop of glacial acetic acid on a slide ; this is used as a microscopical test.

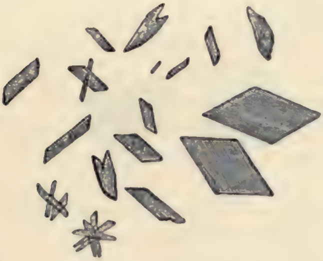

FIG. 4.—CRYSTALS OF HÆMIN (FREY).

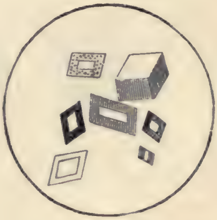

FIG. 5.—CRYSTALS OF HÆMATOIDIN (STEWART).

When reduced hæmoglobin is decomposed by acids or alkalies, oxygen being carefully excluded, it yields **hæmochromogen**, a substance presenting a definite spectrum, and thus a ready means of detecting old blood-stains (see Fig. 2). **Hæmatoporphyrin** is obtained by the action of strong sulphuric acid on hæmatin, which thereby loses its iron ; hæmatoporphyrin is really hæmatin from which the iron has been removed ; it is isomeric with bilirubin. The spectrum of this substance in acid and alkaline solution may be seen in Fig. 2.

Hydrobilirubin is obtained by the action of reducing agents on hæmatin ; it very closely resembles urobilin, a pigment found in urine.

Hæmatoidin (Fig. 5) is found in old blood-clots and in the ovary ; it is a crystalline iron-free product derived from hæmatin, and gives the same reaction with nitrous acid as bile pigment—viz., a play of colours. Hæmatoidin is, in fact, chemically identical with bilirubin, and the name is now of interest merely as indicating the close genetic relationship of the pigments of bile to the colouring matter of blood. Notwithstanding this close relationship, it has not as yet been found possible to convert hæmatin into bilirubin. The nearest approach to bilirubin is iron-free hæmatin (hæmatoporphyrin). Again, both hæmatin and bilirubin may be made to yield an identical product (hydro-bilirubin) ; this product closely resembles urobilin, a pigment found in the urine, and urobilin beyond all doubt is derived from bilirubin in the digestive canal, under the influence of putrefactive organisms.

White Corpuscles, or Leucocytes.—There are certain corpuscles found in the blood, lymph, connective tissue, and pathological products such as pus, which possess a great family resemblance. In the blood they are known as ' white corpuscles,' and it seems quite certain that between the blood and the tissues a free interchange of corpuscular elements occurs ; this process is exaggerated under pathological conditions, as in the case of inflammation and suppuration.

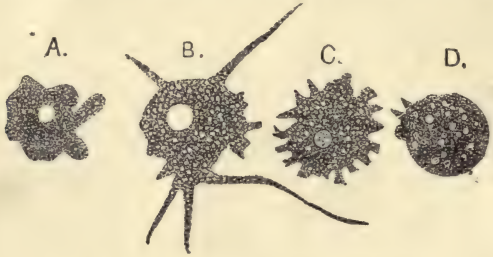

FIG. 6.—AMŒBOID MOVEMENT (STEWART).

A, B, C, D, Successive changes in the form of an amœba.

One characteristic of these cells is their power of spontaneous movement—' amœboid,' as it is termed. In Fig. 6 successive changes in the form of an amœba are shown, and very similar changes occur in these cells. These changes in shape assist materially in the passage of the corpuscle through the walls of the vessels into the tissues. In consequence of their migratory habits these cells are frequently referred to as wandering cells. The white cells of the blood are so called in contradistinction to the coloured or red cells, compared with which they exist in the proportion of 1 to 300 to 1 to 700, depending on the source of the blood. The white cells at the present time are more frequently referred to as blood-leucocytes. They are not all of one kind ; there are microscopical differences in their structure which has enabled a classification to be made, and though this is by no means final, particularly in face of the limited knowledge possessed regarding these cells, yet it is useful as a means of identification and description. Ehrlich regards the white corpuscles as divisible into two main groups—*lymphocytes* and *leucocytes*. The former are distinguished by the cell-body being free from granules, while amœboid movement may be characteristically absent. The opposite condition exists in leucocytes.

Two varieties of **Lymphocytes** are described in the blood—*small* and *large*. The former, the size of a red cell, represents about one quarter of all the white corpuscles ; the latter, two or three times larger in size, do not represent more than 1 per cent. of the whole.

Three varieties of **Leucocytes** are described—*polynuclear*, or *polymorphonuclear*, which represent the bulk of the white blood-cells, with a sub-group known as *eosinophiles* ; *uninuclear* occurring to the extent of from 2 to 10 per cent. of the white cells ; and *mast-cells*, which represent less than 1 per cent. Not only the nature of the nucleus, but also the reaction which the cell granules give with dyes, enables these groups to be distinguished from each other. The granules of the uninuclear cell readily stain with neutral dyes ; the polynuclear cells stain with neutral or acid dyes, while the mast-cells demand basic dyes. Some leucocytes and lymphocytes may be seen in Plate I., 2.

The origin of the lymphocytes and leucocytes has been variously attributed to lymphatic tissue and bone-marrow, but very little is at present known of the subject. There is a free communication between the lymphatic system and the blood via the thoracic duct, and though a mixture of material gains access to the blood by this route, there is no doubt that much of it is pure lymph.

The white corpuscles contain about 10 per cent. of solids. The cell protoplasm consists of proteins belonging to the globulin and nucleo-protein groups, while the nucleus consists of nuclein which is remarkable as being a very stable substance, and also as containing phosphorus. The effect of nucleo-protein when injected into the circulation will be dealt with at p. 21.

The white corpuscles, as well as the red, are constantly being used up and as constantly replaced. They also possess, as we have seen, the power of passing through the walls of the vessels into the surrounding tissues, from which they are removed by the lymph channels, and so find their way back to the blood. No doubt many corpuscles leave the blood, for whose destruction we are unable to account, but it is suggested that by their death they influence the composition of the blood plasma, as in this fluid their component parts must become dissolved after their death.

During the life of the white corpuscle great activity prevails; it is constantly giving up and taking in material which must affect the composition of the plasma. It is known that the white cell possesses the power of digesting certain substances, both solid and liquid. The researches of Metschnikoff have paved the way towards a better understanding of the probable manner in which protection against certain diseases is obtained. He has shown that the white cells take up the bacteria into their interior and digest them, a process termed *phagocytosis;* it is really a fight between bacteria and leucocytes. The difference in the resisting power to disease possessed by 'fit' over 'unfit' animals, and the greater protection afforded by maturity as compared with youth, are facts which may be directly connected with the question of phagocytosis.

The polynuclear cell above described appears to be the leucocyte best adapted to ingesting bacteria, but all are capable of turning out good work, and the thoroughness with which this is done depends upon the composition of the plasma. It appears essential that this should contain a substance which acts upon the bacteria, and renders them an easy prey to the leucocyte. This substance, known as an *opsonin,* may be conveyed to the plasma by the leucocytes, and it may also be artificially increased by the injection into the body of suitable bacteria or of products obtained from them.

It is also probable, as distinct from the doctrine of phagocytosis, that the white cells of the blood may be closely concerned in the production of certain protective substances which destroy bacteria, *bacteriolysins,* the existence of which help to explain the theory of immunity.

Coagulation.—We are now brought to a consideration of the subject of blood-clotting, a process by which the naturally fluid blood becomes converted into a solid.

If blood be drawn from the body and left at rest, it will be found within a few minutes to have undergone the process of clotting. The fluid first becomes a jelly and then a firm clot or crassamentum, taking a complete cast of the vessel in which it is placed, and so firm in consistence that it may be inverted without any blood being lost. In a short time the clot begins to contract, and by so doing squeezes out a fluid known as *serum* (Fig. 7). This gradually accumulates, and as it becomes abundant the clot sinks. The blood of the horse is remarkable for the slow rate at which coagulation occurs, and the red cells, being specifically heavier than the plasma, have time to fall in the fluid before the process is completed. The result of this is that the upper solid layer is considerably decolourized, forming the so-called **buffy coat,** which, though natural to the blood of the horse, is indicative in other animals of the presence of an inflammatory process in the system.

We have here closely followed the account given by human physiologists of the coagulation of the blood in the horse, but the appearance described is by no means invariable. Coagulation in this animal is often complete in less than five minutes, when, of course, no buffy coat forms, and we are inclined to believe that rapid coagulation and non-buffy coat are the rule rather than the exception; we have repeatedly observed the blood of the horse clot so rapidly as to be almost instantaneous. One thing in connection with horse's blood is undoubted, and that is that coagulation is more easily slowed or prevented by cold and neutral salts than it is in the blood of any other warm-blooded animal. May it not be that some confusion has thus arisen, and we have come to regard this abnormally easy slowing of clotting by cold and salts, as if it were markedly a characteristic of horse's blood as it clots naturally?

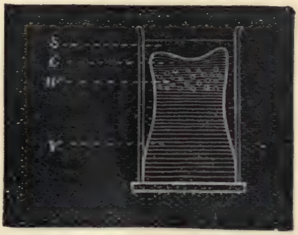

Fig. 7.—Diagram of Clot with Buffy Coat (Stewart).

v, Lower portion of clot with red corpuscles; *w*, white corpuscles in upper layer of clot; *c*, cupped upper surface of clot; *s*, serum.

According to Nasse, the average time occupied in coagulation is as follows:

Pig	½	to	1½	minutes.
Sheep	½	,,	1½	,,
Dog	1	,,	3	,,
Ox	5	,,	13	,,
Horse	5	,,	13	,,

In our experience the extreme time mentioned for the horse is exceptionally long.

If the clot be examined microscopically, it is found to consist of fine fibrils, entangled in which are the blood corpuscles; if the fibrin produced be washed completely free from blood, its appearance is well described by its name.

If instead of allowing the blood to clot spontaneously it be whipped with a rod or bunch of twigs, or, as we say, is 'defibrinated,' the fibrin separates rapidly and coats the rod, while no coagulation in the remaining fluid can occur. The power of spontaneous clotting lies, then, in the production of fibrin.

These changes may be graphically represented thus :

On Clotting.

Blood.	Plasma.	Serum.	
		Fibrin.	Clot.
	Corpuscles.	Red.	
		White.	
		Blood platelets.	

When Whipped.

Blood.	Plasma.	Fibrin.	
		Serum.	Defibrinated blood.
	Corpuscles.	Red.	
		White.	
		Blood platelets.	

Fibrin is a yellowish-white, stringy-looking, bulky mass. Its bulky appearance would lead to the belief that it exists in blood in large quantities ; it is found, however, to be by weight relatively small (0·2 to 0·4 per cent.).

The cause of coagulation has kept physiologists busy for many years, and even at the present time the matter has by no means been settled. The theory most generally accepted is that of Hammarsten—viz., that clotting is due to the conversion of a fluid fibrinogen into a solid fibrin, under the influence of a substance spoken of as fibrin ferment.

If blood be prevented from coagulating, plasma can be obtained, and this plasma, depending upon the agents used in its production, will teach the main facts of coagulation. If it be obtained by cooling the blood, then the plasma will clot spontaneously by allowing the temperature to rise ; if the plasma be obtained by previously mixing the blood with a definite amount of magnesium sulphate or common salt, clotting will occur on diluting it. If it be obtained by acting on blood with oxalates, then clotting can be brought about on the addition of a lime salt. The clot formed by the plasma coagulating is precisely the same as that formed by the blood coagulating ; it is, of course, colourless.

If the above plasmas be acted upon by adding common salt to half saturation, a precipitate of **fibrinogen** occurs ; this is a protein belonging to the globulin group, and has previously been alluded to. If this precipitate be redissolved by diluting the fluid, and allowed to stand, it clots spontaneously. If a solution of pure fibrinogen be prepared, it does not clot spontaneously, but it may be made to do so by the addition of a drop of serum or the washings of a blood-clot.

The substance which brings about coagulation of the blood is contained in the plasma; it is not found in the serum, as shown by the fact that the latter is incapable of spontaneous coagulation. The difference between plasma and serum, as we have already seen, is that the former contains fibrinogen and the latter does not.

Nor is clotting a function of the red cells, for lymph is capable of clotting, and there are no red cells in it; and, further, there is an abundance of red cells in defibrinated blood, yet clotting is impossible.

We have previously learnt that in the plasma both fibrinogen and serum-albumin are present; the evidence that serum-albumin takes no share in the process of clotting is that serum contains an abundance of serum-albumin, yet spontaneous coagulation is impossible.

Everything points to the fluid fibrinogen of the plasma being converted into the solid substance fibrin, and in whatever other respects physiologists differ regarding the question of coagulation, all are agreed on this fundamental fact. In the observations above described it has been shown that a solution of pure fibrinogen does not clot spontaneously, but that it at once coagulates on the addition of a drop of serum or washed blood-clot.

From this fact we learn that the conversion of fluid fibrinogen into solid fibrin cannot occur without the agency of another substance. The fibrinogen will not coagulate of itself; it requires to be rendered active by something contained in a drop of serum or a washed blood-clot. This substance is generally spoken of as **fibrin ferment**; its present-day name is **thrombin**. The term 'ferment' was employed since in some respects the substance resembled the class of bodies known as 'ferments,' inasmuch as a very small amount appeared to be capable of acting on an indefinite amount of fibrinogen; it further resembled a ferment in its action, being closely dependent on temperature. It is now, however, more generally believed that a small amount of the ferment will not act upon an indefinite amount of fibrinogen, the amount of fibrin formed being proportional to the amount of ferment present.

It was stated above that a drop of serum added to a solution of fibrinogen at once causes clotting. Evidently, then, blood-serum contains in abundance the substance known as 'fibrin ferment' or 'thrombin.' If the serum be boiled or heated to 65° C. (150° F.), a drop of it added to a solution of fibrinogen does not cause clotting; but this function can be restored by the addition to it of an alkali. This observation should largely, if not entirely, exclude thrombin from being classed as a ferment.

A drop of stale serum will not produce clotting with fibrinogen. The reason why stale serum refuses to act is unknown.

Thrombin may readily be prepared by extracting a dried blood-clot with water. The addition of a few drops of this extract to hydrocele or pericardial fluid at once causes coagulation, for these fluids contain fibrinogen, but no ferment. Thrombin is a colloid, and its resistance to putrefaction suggests it is not a protein substance. According to some observers, thrombin is present in the circulating blood, but if blood be received with special precautions directly from an artery into a large bulk of alcohol, the clot, when dried and extracted as above, yields no thrombin. It seems reasonable to infer that the blood does not coagulate in the vessels during life, as there is no thrombin present. Nevertheless, if solutions of thrombin are injected into the circulation they do not produce intravascular clotting with the certainty that might be expected, and it has been suggested that in such cases the thrombin has been destroyed in the liver, but the evidence of this is not convincing. We shall look at the question again.

If thrombin does not exist as such in the blood-stream, to what is its origin to be attributed ? Blood received direct from the vessels into a solution of oxalate of soda will remain indefinitely uncoagulated, but the addition of calcium chloride at once causes clotting. This result was originally explained by saying that the lime in the blood was thrown out of solution by the oxalate, and that the addition of calcium caused coagulation. But an oxalate solution of fibrinogen is coagulated by an oxalate serum containing thrombin. Evidently, therefore, in the first of these two experiments thrombin was absent, and in some way or other was produced by the addition of calcium chloride. It is now supposed that the calcium is not concerned in the action of the thrombin on fibrinogen, but that its function is to assist in the production of thrombin from some antecedent substance. To this substance the name **pro-thrombin** or **thrombogen** has been given. According to some views, this substance exists in living blood, while others regard it as a product of the breaking down of the platelets and leucocytes of the blood after the latter has been shed.

If both thrombin and pro-thrombin are formed after the blood is shed, what is it that stimulates the production of pro-thrombin ? One view which finds many supporters is that the pro-thrombin is liberated from the disintegrating blood-cells by the action of a kinase,* **thrombokinase**, which, together with calcium salts, converts thrombogen into thrombin.

Another view is that the circulating plasma contains thrombogen, but not thrombokinase, the latter being liberated from the leucocytes and blood platelets after shedding. In the presence of calcium, thrombokinase converts thrombogen into thrombin.

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* *Kinases* are activating substances.

Not only is thrombokinase present in the above cellular elements of the blood, but it exists in all the tissues of the body. The practical importance in the case of a wound of having thrombokinase at hand to act on the thrombogen, and so cause coagulation by the production of thrombin, is very evident, for the cessation of hæmorrhage is due to the formation of fibrin in the mouths of the vessels.

There is a substance known as 'nucleo-protein,' readily obtained from tissue-cells, thymus, kidney, lymphatic glands, and other organs, which is very closely identified with thrombin. If nucleo-protein be prepared, and a large dose injected into the veins of an animal, intravascular clotting and death at once occur. On the other hand, if a small dose be injected, no such effect is produced—in fact, the blood is rendered uncoagulable. To this phenomenon the term 'negative phase' has been applied, in contradistinction to the positive phase in which clotting at once occurs. The explanation which has been offered of the negative phase is that an *antibody* is produced which neutralizes the thrombokinase. But it has also been held that two different substances are obtainable from the above tissue-cells—one, *leuconuclein*, which accelerates, and the other, *histon*, which retards coagulation; whichever effect is observed is said to depend upon the relative amount of each present.

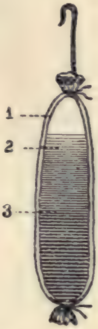

Fig. 8.—Vein of a Horse tied between Two Ligatures.

1, Plasma; 2, white corpuscles; 3, red corpuscles.

The view that an antibody exists in living blood which prevents coagulation in the vessels is urged by some. Such an antithrombin has not at present been extracted from the inner wall of the bloodvessels, but the theory offers an explanation, not only of why blood remains fluid during life, but also of the fact that coagulation of the blood in the vessels after death is a slow process. It also offers a reasonable explanation of a very old experiment on the horse, in which the jugular veins, occluded by ligatures and excised, maintains the enclosed blood in a fluid condition for one or two days, so long as it is left in contact with the wall of the vessel; clotting, nevertheless, at once occurs on removal. Fig. 8 shows diagrammatically this so-called 'living test-tube' experiment, the explanation of which was for years attributed to the influence exerted in some way or other by the normal endothelium of the vessel on the contained blood.

Intravascular clotting may occur under pathological conditions, as when the inner coat of the bloodvessel is injured, and the cells then act as a foreign body. This may be seen in a ligatured vessel, while pathologically the horse provides a classical example in the injury occurring to the iliac arteries, which leads to thrombosis.

Circumstances influencing Coagulation. — Clotting in shed blood may be retarded or hastened by certain conditions. The blood of a horse received into a vessel so constructed as to expose it to a *freezing temperature* may be kept fluid for an indefinite period, though coagulation will at once occur when the temperature is allowed to rise. The probable explanation of the phenomenon is that the low temperature keeps the corpuscles from disintegrating.

Clotting is delayed by the addition to the blood of certain *neutral salts* of the alkalies and alkaline earths ; the best salt to employ for the purpose is magnesium sulphate. The plasma so obtained is spoken of as salted plasma, and largely used in physiological experiments on the blood. It is not known how neutral salts prevent coagulation ; it may be by keeping the corpuscles intact, or by inhibiting the conversion of prothrombin to thrombin. The addition of dilute *acetic acid* or the passage of a current of *carbonic acid gas* through blood prevents coagulation by precipitating fibrinogen. The addition to blood of a weak solution of *potassium* or *sodium oxalate* prevents clotting by combining with lime. Without the presence of calcium, thrombogen cannot, as we have seen, become converted into thrombin ; if, however, a soluble calcium salt, be added, the power of clotting is restored. *Sodium fluoride* has much the same effect on blood as sodium oxalate: it combines with the lime ; but the power of clotting is not restored by merely adding a soluble calcium salt. Some tissue extract must also be included, for the fluoride has interfered with the action of the thrombokinase.

The action of certain *organic substances* in retarding blood-clotting is very remarkable. If *peptone* be injected into the blood of a dog, such blood will not clot ; it can be shown that this is not directly due to the action of the peptone, for the latter may be added to blood without inhibiting coagulation. Peptone introduced into the circulation causes the secretion in the liver of a substance which prevents blood-clotting, an antithrombin. *Leech extract* contains a similar substance. This antithrombin—designated *hirudin*—is secreted by the salivary glands of the leech. When an extract of these is injected into the circulation, the blood loses its power of clotting, and, unlike peptone, leech extract, when added to blood drawn from the body, prevents coagulation. The bleeding following leech-bites and the fluid condition of the blood in the body of the leech are due to the action of this antithrombin.

Clotting of blood is retarded if the fluid as shed is received into a vessel the wall of which is thinly coated with oil. The shape of the collecting vessel has also an influence over coagulation, clotting being much slower in a deep, smooth vessel than in a rough, shallow one. By increasing the foreign surface to which the blood is exposed clotting is hastened. This is the explanation of the influence of washing a bleeding wound, and the application of compresses excites in some way or other the formation of thrombin.

The **Extractives** of the blood are fats, cholesterin, lecithin, kreatine, urea, hippuric acid, uric acid, and grape-sugar, all in small and varying quantities. The amount of fat in the blood during digestion is 0·4 to 0·6 per cent. ; in dogs fed on a fatty diet it may reach 1·25 per cent., and may give the serum a milky appearance. There is twice as much fat in the serum of recently-fed horses as in the serum of those kept starving. Other extractives such as soaps are found to the extent of 0·05 to 0·1 per cent. ; urea, 0·02 to 0·04 per cent. ; sugar, 0·1 to 0·15 per cent. The corpuscles contain neither sugar nor fat, and possess a larger amount of cholesterin and lecithin than the plasma.

The characteristic **Difference between Arterial and Venous Blood** is that the former contains more oxygen and less carbonic acid, though there is always, in fully arterialised blood, about twice as much carbon dioxide as there is oxygen (see p. 122). Arterial blood also contains more water, fibrinogen, extractives, salts, and sugar, fewer blood corpuscles, and less urea ; its temperature is, on the average, 1° C. lower. The dark colour of venous blood is not due to the greater amount of CO_2 it contains, but to the diminution of oxygen in the red blood-cells. The alteration in colour effected by the addition of reagents and gases to blood is probably due partly to alterations in the shape of the corpuscles themselves, which become more concave on the addition of oxygen and less concave on its removal, and also to the fact that oxyhæmoglobin is brighter in colour than reduced hæmoglobin.

The **Salts** of the blood are divided between the plasma and the corpuscles. The distribution of these is not the same in all animals ; in the horse and pig, for example, sodium only exists in the plasma and none in the corpuscles, while in both animals the potassium in the corpuscles is very high ; in the ox and dog both corpuscles and plasma contain sodium. Sodium chloride is the most abundant salt of the blood, potassium chloride and sodium carbonate come next, and lastly phosphates of calcium, magnesium, and sodium. The chief inorganic substance of the cells is potassium phosphate. The following table from Bunge bears on the question of the salts of the blood in different animals:

	1,000 grammes of corpuscles contain—			1,000 grammes of serum contain—		
	K.	Na.	Cl.	K.	Na.	Cl.
Horse -	4·920	0	1·930	0·27	4·43	3·750
Ox -	0·747	2·093	1·635	0·254	4·351	3·717
Pig -	5·543	0	1·504	0·273	4·272	3·611

Water free from salts is destructive to protoplasm; no doubt, therefore, one important function of the salts in the blood is to maintain the vitality of the tissues. Sodium chloride is here especially valuable, and its extensive presence in blood (60 per cent. to 90 per cent. of the total amount of ash) corresponds to its importance. As the blood is simply the carrier of the salts, and the only channel by which the tissues can obtain them, it by no means follows that all the mineral matter found in it is essential to its own repair and constitution.

The **Temperature of the Blood** in the different domestic animals varies from 37·8° C. to 40·54° C. (100° to 105° F.), the warmest blood in the body being found in the hepatic veins.

The **Quantity of Blood in the Body** cannot be determined by mere direct bleeding alone. After all the blood is drained off, the vessels require to be washed out, and the quantity of blood in the water estimated by the colour present; the body has then to be minced and macerated, and the quantity of blood in this estimated by the colour test, comparison being made with a standard solution of blood.

By Haldane and Lorrain Smith's carbon monoxide process the amount of blood in the living animal may be calculated. The essential steps in this process are to estimate first colorimetrically the percentage of hæmoglobin in the blood, and then the extent to which this is saturated by breathing a measured volume of carbon monoxide. In this way the total capacity of the blood for carbon monoxide may be ascertained, and the carbon monoxide capacity being the same as the oxygen capacity, the volume of the blood may be readily calculated.

Sussdorf* puts the proportion which the weight of the blood bears to the body weight as follows:

Horse - $\frac{1}{15}$ = 6·6 per cent. of the body weight.
Ox - $\frac{1}{13}$ = 7·71 ,, ,, ,,
Sheep - $\frac{1}{12}$ = 8·01 ,, ,, ,,
Pig - $\frac{1}{22}$ = 4·6 ,, ,, ,,
Dog - $\frac{1}{11}$ = to $\frac{1}{18}$ = 5·5 to 9·1 per cent. of the body weight.

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* Ellenberger's 'Physiologie der Haussäugethiere.'

The same observer gives the amount of blood in the body of the horse at 29 litres (66 pounds, or nearly 50 pints).

The **Distribution of Blood in the Body** (Fig. 9) is believed to be as follows:

About one-fourth in the heart, lungs, large vessels, and veins.
,, ,, liver.
,, ,, skeletal muscles.
,, ,, other organs.

It is probable that in the horse the liver would contain less than one-fourth the bulk of blood, while the skeletal muscles would contain more. Under certain conditions the abdominal veins are capable of containing the whole of the blood in the body. When an organ is active it receives more blood than when in a state of rest; this increase has been variously estimated at from 30 to 50 per cent.

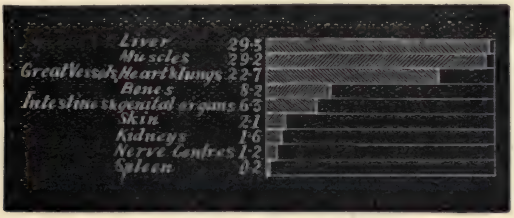

FIG. 9.—DIAGRAM TO ILLUSTRATE THE DISTRIBUTION OF THE BLOOD IN THE VARIOUS ORGANS OF A RABBIT, AFTER RANKE'S MEASUREMENTS (STEWART).

The numbers are percentages of the total blood.

Regeneration of the Blood after Hæmorrhage.—Regeneration of the fluid portions of the blood is extremely rapid, experiments showing that after slight hæmorrhage the normal volume is regained within a few hours, and after severe hæmorrhage in from twenty-four to forty-eight hours. This is supported by clinical observation; in the days of severe bleedings venesection to the extent of producing syncope was frequent, yet in a very short time the volume was restored. In these cases it is the plasma which is rapidly replaced. The red cells and hæmoglobin take longer to prepare, probably several days, perhaps even two or three weeks. In the dog exact observation shows that a hæmorrhage of from 2 to 3 per cent. of the body weight is readily recovered from, while a loss of 4·5 per cent., which represents half the blood in the body, is generally fatal. Percivall tells us* that in the horse he occasionally drew 3 gallons of blood, which may be taken as half the amount in the body, apparently without fatal consequences.

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* 'Hippopathology,' vol. i., p. 95.

Transfusion of warm normal or physiological saline solution (NaCl 0·9 per cent.) is capable of keeping the heart beating even after severe hæmorrhage, showing that the immediate essential factor is the restoration of bulk to the empty vascular system. Transfusion of blood is not without danger, for, as has been shown in dealing with hæmolysis, the serum of one animal may be toxic to another.

The **Gases of the Blood** are more conveniently dealt with in the chapter on Respiration (see p 121).

Composition of the Blood.—Reviewing the various analyses which have been published of the blood of animals, the following represents the average composition of the fluid :

The Plasma.

Water	90 parts per cent.
Proteins	8 or 9 parts.
Fats	0·1 part.
Extractives	0·4 ,,
Salts	0·8 ,,

The Corpuscles.

These represent from one-third to half the weight of the blood, and consist of—

Water	64 parts per cent.
Solids	35 ,, consisting of 32 per cent. hæmoglobin, 0·1 per cent. proteins.
Salts	1 part.

Taking the blood as a whole, the following represents approximately its composition in every 100 parts :

Water	81 parts.		
Solids	19 ,,	Hæmoglobin	13 parts.
		Proteins	4 ,,
		Salts	1 ,,
		Extractives	0·6 ,,

The Blood in Disease.—The blood plays two distinct parts in disease : it is a carrier and distributer of infection to the body-cells, and, further, it may itself undergo profound pathological change.

All the specific infective diseases of animals are spread through the body by means of the blood-stream. It is true that the initial source of entry may be an allied passage—the lymph-stream—but it is by means of the blood that the final and complete invasion of the body is effected. Nor does this observation apply to specific diseases only ; if we take two such opposite conditions as anthrax and poisoning by arsenic, it is the blood in each case which is responsible for the distribution of the infecting agent.

The blood-tissue itself may be the seat of disease ; micro-organisms may live and multiply in the plasma, and infect the whole body as in anthrax. Some of the organisms may be so small as to be ultra-microscopic, and in connection with this question some of the most acute and fatal infectious diseases of animals are caused by organisms of this class, of which rinderpest, foot and mouth disease, rabies, and African 'horse sickness' are examples. Still, in spite of the fact that these microbes have not been seen, their existence is undoubted, the best evidence of which is that some of them are sufficiently large to be caught in the pores of a filter, leaving the filtrate sterile. Other organisms attack the blood-cells, either from without or within—for example, the important group of Trypanosomes, the malaria parasite, the organism of Texas fever, and such like. In these cases the product of red-cell destruction may show itself by the discoloured urine, and is evident in the tissues—for example, the liver and spleen.

Compared with the red corpuscles, the white are seldom affected with disease, but there are certain pathological conditions associated with a great increase in their number (*leucocytosis*), and others in which the white cells are reduced in number (*leucopænia*).

There are other conditions affecting the blood—for instance, *Purpura*—which cannot be attributed to parasitic agency. In this disease, either from defects in the blood or vessel-wall, hæmorrhage takes place into the tissues. No organ appears to be able to escape, though probably the subcutaneous and muscular tissues are the most frequent seat of the hæmorrhage.

Quite as strange and obscure is the dietetic disease of equines known as hæmoglobinuria, in which the animal in the middle of work suddenly falls paralysed; the urine becomes coffee-coloured and loaded with methæmoglobin, in consequence of the destruction of the red cells. What the destructive agent is, is at present unknown, but it is probably one of the poisonous products of proteid disintegration, which will be found dealt with in the chapter on Digestion.

Blood-letting in the treatment of disease was at one time so universal that it came to be regarded as the 'sheet-anchor' of life, and animals were regularly bled in *order to keep them in health.* 'Blood-letting' was killed by abuse; it is now a question whether the pendulum has not travelled too far in the other direction, and the employment of a physiological means in the treatment of disease been too long neglected. Towards the end of the eighteenth century a full blood-letting for the horse was from 4 to 5 pints. During the first half of the nineteenth century 8 pints were considered a moderate bleeding. Under pressure of acute disease 3 gallons were drawn, and Percivall tells us he had heard of 4 gallons being taken (see p. 25).

This is the abuse we allude to as having caused the fashion to change. Such heavy blood-lettings must have been responsible for considerable mortality. Percivall describes the 'impression on the system,' which was considered a necessary indication if blood-letting was to prove beneficial. As the pulse began to sink, the horse became very uneasy, jerking the head up and down, moving backwards until finding support for the hind-quarters; respirations increased, deep sighing, the body rocking from side to side, in danger of falling headlong; shivering; and, after the operation, sweating. A second and even third bleeding was employed.

The effect of bleeding healthy animals to improve nutrition was fully accepted, and Percivall declares his opinion that, if continued in, it became necessary for preserving health. An increased disposition to fatten was observed in young animals submitted to moderate bleeding, and farmers employed this regularly for their calves.

CHAPTER II

THE HEART

THE blood in the body has to be kept in constant motion, so that the tissues which are depending upon it for their vitality may be continuously supplied, and also in order that the impure fluid resulting from the changes in the tissues may be rapidly and effectually conveyed to those organs where its purification is carried out.

The heart is the organ which pumps the blood over the body, not only distributing it to the tissues, but forcing it on from these back to the heart again, to be prepared for redistribution. It may be described as a hollow muscle divided into two compartments, usually known as right and left, but in quadrupeds really anterior and posterior, each compartment being divided into an upper half or auricle, and a lower or ventricle. Opening into the auricles are large veins which convey the blood back to the heart, while from the ventricles other vessels, arteries, take their origin for the conveyance of blood from the heart. The auricles and ventricles are separated by a valvular arrangement, and the two sides of the heart are separated by a muscular partition (Fig. 10).

So far the general arrangement of both right and left sides is much the same, each having to receive and then to get rid of a certain quantity of blood sent into it. But the blood sent into the right side of the heart is very different from that received by the left, and with this difference we must for a moment deal. The whole of the impure or venous blood in the body is brought into the right side of the heart for the purpose of being distributed to the lungs, where it is purified; into the left heart this arterial or purified blood is brought back from the lungs for distribution to the body. The passage of the impure or venous blood from the right side of the heart through the lungs to the left side is known as the *Pulmonic* circulation; that of the blood, thus purified, through the body and back to the right side of the heart is called the *Systemic* circulation (Fig. 11).

Mention has been made of *valves* in the cavities of the heart ; they are found on both sides separating auricle from ventricle, and are known as the right auriculo-ventricular or tricuspid valve, and the left auriculo-ventricular or mitral valve. Besides these, valves are found in the vessels arising from the ventricles—viz., in the pulmonary artery and the aorta ; these valves, pulmonary and aortic, are known as the semilunar valves. No valves are found guarding the entrance of the vessels (veins) into the auricles. In order to understand the function of these valves, which play such an important part in the physiology of the heart, it is necessary that we should briefly detail the course which the blood takes from the time it enters the right auricle until it completes the round of the circulation and finds itself at this auricle again.

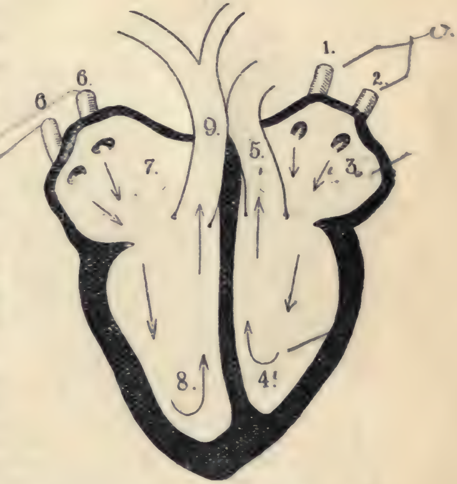

FIG. 10.—DIAGRAM OF THE CIRCULATION THROUGH THE HEART.

1 and 2, The venæ cavæ ; 3, right auricle ; 4, right ventricle ; 5, pulmonary artery ; 6, 6, pulmonary veins ; 7, left auricle ; 8, left ventricle ; 9, aorta dividing into anterior or posterior. The arrows represent the direction taken by the blood-stream.

Course of the Circulation.—The venous blood from the whole of the body flows into the right auricle by means of the anterior and posterior venæ cavæ ; it passes from here through the tricuspid valve into the right ventricle ; from the right ventricle it travels to the lungs by means of the pulmonary artery, where, having been exposed to the action of the air and become greatly changed in its gaseous composition, it returns to the heart by means of the pulmonary veins, emptying itself into the left auricle. It now passes through the auriculo-ventricular opening into the left ventricle, and thence into the aorta to be pumped all over the body, being distributed by means of the arteries and capillaries ; it is then collected by the veins, and eventually brought back to the heart to undergo afresh its distribution to the lungs and body (Fig. 11).

The use of the valves is to allow of and to insure the transference of blood from auricles to ventricles, and from the ventricles to the aorta and pulmonary artery without any chance of regurgitation. This they do in virtue of the fact that they are so constructed and arranged as to open only in that direction towards which the blood has to be sent.

Position of the Heart.—The heart occupies a position in the middle line of the chest, and is suspended from the spine by means of its arterial trunks. These are its only means of support. Some help may be afforded by its connection with the root of the lungs; but in thinking of the heart as a pump it must be remembered that all the movements it executes in its constant work are carried out as the organ literally hangs from the spine. It rests on nothing; the apex is clear of the sternum; the pericardium keeps it in its place, but is no mechanical aid in keeping it in position. In the dog the pericardium obtains attachment to the diaphragm, but not so in the horse and ruminants. Further, in the dog and cat the heart rests on the upper face of the sternum, whereas in the horse it does not touch the sternum. Fig. 12 gives an accurate notion of the position of the heart. It will be observed that the organ is tilted forward, the base lying in front of the apex.

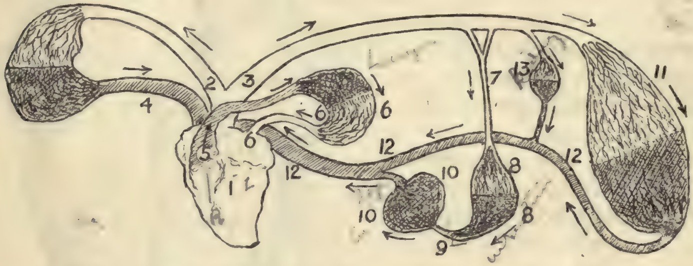

FIG. 11.—DIAGRAM OF THE CIRCULATION OF THE BLOOD.

1, The heart; 2, anterior, 3, posterior aorta; 4, anterior vena cava; 5, pulmonary artery; 6, pulmonary veins; 7, mesenteric arteries; 8, intestinal capillaries; 9, portal vein; 10, the liver, the veins from which open into (12) the posterior vena cava; 11, the circulation through the hind extremities; 13, the circulation through the kidney.

The base of the heart is uppermost, and the organ in the horse occupies a position corresponding to the third, fourth, fifth, and sixth ribs. It is between the fifth and sixth ribs, just above their sternal insertion, that the impulse of the heart can be felt. On its right face is the right lung, and on its left part of the left lung, the big triangular notch in which exposes the left ventricle and enables it to make its impulse felt against the chest-wall. The anterior face of the heart is formed by the right auricle and ventricle, the posterior by the left auricle and ventricle. The pulmonary artery runs along the left face, and the posterior vena cava lies on the right face.

Heart Muscle.—The heart muscle in structure is considered to come midway between skeletal and involuntary muscle. Until recently its fibres were described as short, branching, anastomosing, and possessing no sarcolemma. There is good reason to believe that this account is no longer correct, and that the fibres, instead of being short, form a continuous sheet, fibrils passing from fibre to fibre, and so constituting an anastomosis in every direction. There is evidence also that a sarcolemma is present, though it is delicate in structure. The fibrils, or sarcostyles, of which the fibres are composed, are both longitudinally and transversely striated.

Fibres, described as the *fibres of Purkinje,* are found beneath the endocardium of the horse, ox, and sheep. They give a greyish appearance to the part, and on microscopical examination are found to be large polyhedral, clear cells, containing granular substance and one or more nuclei. These fibres are connected with a peculiar band of muscle which forms a connection between the auricle and ventricle. This band or bundle is known as the **Auriculo - ventricular** or **A.V. Bundle**, and is the discovery of recent years. Prior to that it was held that the muscular structure of the auricle and ventricle was distinct, the chambers being separated by a fibrous ring ; but in the heart of the ox and sheep this bundle of muscle connecting the auricle and ventricle can easily be traced by its paleness. This is proved to hold good for all mammalian hearts.

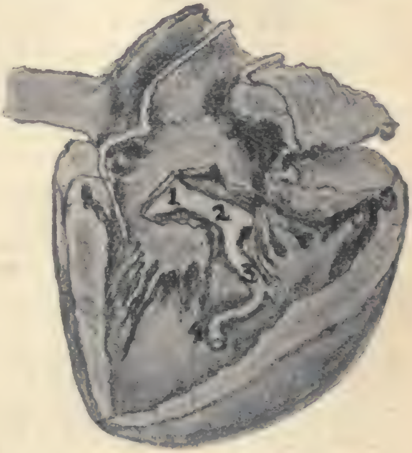

FIG. 12.—RIGHT AURICLE AND VENTRICLE OF CALF, TO SHOW AURICULO - VENTRICULAR BAND (AFTER KEITH).

1, Auriculo-ventricular (A.V.) node ; 2, main auriculo-ventricular bundle ; 3, right septal division of the bundle ; 4, moderator band.

In Fig. 12 may be seen the arrangement of the band in the right auricle, where it begins as a swelling known as the *A.V. Node* (1). This node microscopically is found to consist of peculiar branched cells.

From the node is given off the main bundle (2), and the latter divides into right and left divisions, one running to the right ventricle and one to the left. The right heart bundle (3) runs downwards into the ventricular septum, and is distributed to the *musculi papillares* and moderator bands. In the left heart the bundle reaches the left ventricle from the right auricle; it then runs down the ventricular septum, and, like its fellow in the opposite side of the heart, is distributed to the *musculi papillares* and moderator bands.

The **muscular walls of the auricle and ventricle** are constructed of layers of red fibres, varying greatly in thickness and of extremely complex disposition, especially around the ventricular cavities. The ventricular walls are thicker than those of the auricles, and the left side of both cavities is better developed than the right. In certain portions of the right auricle the wall is so thin as to be semi-transparent, and appears, in fact, to consist of little else than the two layers of serous membrane which cover and line the heart. The ventricular walls are of uneven thickness; at the apex of the heart they are reduced to a few fibres of muscular tissue one-eighth of an inch in thickness. Chauveau, in fact, says that at this point there is nothing more than two layers of serous membrane—viz., that lining and that covering the heart.

The varying thickness of the walls of the heart is due to the complex arrangement of the various layers of fibres; these may, broadly speaking, be divided into two main groups—an internal, belonging to each auricle and each ventricle separately, and an external group, belonging to both auricles and both ventricles. Excluding the A.V. bundle just described, the fibres of the auricles are confined to the auricles, and the fibres of the ventricles to the ventricles; the advantage gained by this arrangement is obviously connected with the independent contraction of auricles and ventricles.

The muscular layer peculiar to each ventricle is very complex, but, generally speaking, may be described as a scroll of fibres of several layers running obliquely around each ventricle, and where the scrolls meet forming the ventricular septum. The scrolls are attached above to the auriculo-ventricular ring, but are left open below. If we can imagine these scrolls separated from the other muscle of the heart, they would present the appearance of a pair of hollow cones. Covering this internal layer is an external, belonging in this case to both ventricles; it takes its origin from the auriculo-ventricular ring, and describes a spiral course in descending from base to apex of the heart, where the fibres form what Henle described as a vortex (Fig. 13); they then pass upwards through the opening in the scrolls of the inner layer, and so gain the interior of the ventricles. Some of the fibres pass to the *columnæ carneæ*, others to the *musculi papillares*, while the majority gain insertion into the auriculo-ventricular ring from which they had their origin. As pointed out by

Chauveau, whose account of the arrangement of the fibres in the heart of the horse we have mainly followed, this layer forms between its origin and insertion figure of eight loops, the smallest loop being at the apex of the heart, where at its centre it leaves a very small space, through which a probe may be passed into the ventricles without piercing anything but the external and internal layer of serous membrane. The external fibres of the right ventricle are arranged much the same as those of the left, but, according to Pettigrew, they do not pass into the ventricle at a single point as in the left ventricle, but obtain entrance all along the anterior coronary groove.

The fibres of the auricle are much simpler in their arrangement. Those peculiar to each cavity are disposed in several fasciculi, some circular, especially surrounding the mouths of the vessels, others in the general body of the auricle in interwoven loops. The septum is formed where the two sets proper to each auricle meet. The fibres common to both auricles are generally arranged transversely.

It may be added that anatomists are not agreed as to the arrangement of the fibres of the heart muscle, and this may to some extent be due to the fact that the system is not the same in all animals.

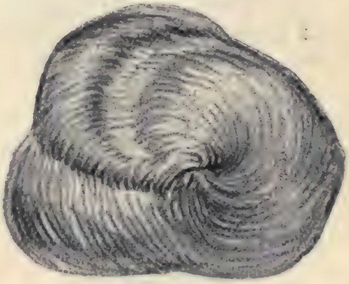

FIG. 13.—APEX OF HEART, SHOWING VORTEX ARRANGEMENT OF FIBRES (AFTER KRAUSE).

The arrangement just outlined certainly appears to provide for the squeezing and wringing movement to which the ventricular contents are exposed, the shortening of the heart wall from base to apex, and the contraction of the *musculi papillares* at the moment the valves close. Far simpler is the disposition of the muscular fibres of the auricles; physiologically these cavities may be regarded as the dilated extremity of the vessels entering the heart, and their function is more that of a well than a pump. Nevertheless, the existence of a network of muscular pillars in the auricles, especially the dense bands in the left, warn us to be careful not to regard these cavities in the horse as mere passive channels of the circulation.

The cavities of the heart are lined by the endocardium which is reflected over the valves; this membrane in the left auricle of the horse is of a peculiar grey colour.

Certain fibrous rings are found in the heart where the valves are situated, to which these and the muscular fibres obtain a firm attachment. The ring surrounding the aortic opening in the ox has constantly in its substance one or more pieces of bony tissue ; this is also common in the horse.

Valves of the Heart.—The *auriculo-ventricular* valves are made up of fibrous membrane, in which a small proportion of muscular fibre is found close to the attached border. The *mitral* or *bicuspid* valve in the horse consists of one large distinct segment, and several smaller ones united to form a second ; the tricuspid consists of three segments, one, much larger than the others, being placed opposite to that portion of the ventricle which leads to the pulmonary artery.

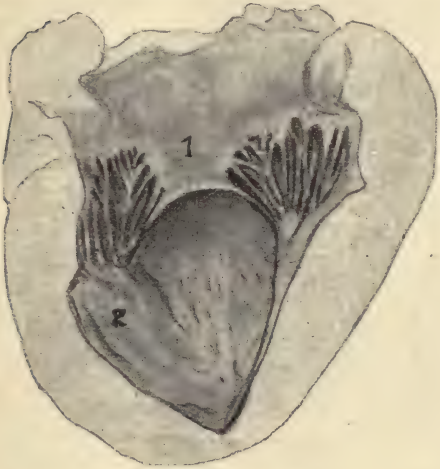

FIG. 14.—LEFT VENTRICLE OF HORSE EXPOSED TO SHOW MITRAL VALVE.

1, Portion of valve ; 2, *columnæ carneæ*, on the upper surface of which are found the *musculi papillares*, to which the *chordæ tendineæ* are attached.

The free edges of all the valves are held in position by large and small tendinous cords (*chordæ tendineæ*) composed of fibrous tissue, which are inserted into *musculi papillares* found on the internal surface of the ventricle ; the cords from one papilla do not all pass to one segment of the valve, but to two or three (Fig. 14). The function of the papillæ is to restrain the valves from being forced too far into the auricle during the contraction of the ventricle, and this they accomplish by gradually shortening as the walls of the ventricle approximate ; compensating by their shortening for the movement of the ventricular wall, and thus exerting traction on the cords (Fig. 15). This shortening is brought about by the layer of muscular fibres which at the apex passes from the external face of the heart into the interior of the ventricles, and thence to the fleshy columns and papillary muscles (p. 32). Other bands pass from one side of the ventricle to the opposite wall ; they are called *moderator bands*, and their function is to protect the ventricular wall from undue distension.

The valvular flaps meet in the most perfect apposition when the ventricles contract ; their edges are inverted, and the sides of the valves curl in and lie so close to their fellows that nothing can escape upwards into the auricles (Fig. 16). This may be readily demonstrated in the dead heart by tying the aorta and pulmonary veins, and introducing into the left auricle a tube which admits a powerful jet of water; the left side of the heart distends and hardens, and at last water forces its way out of the hole in the auricle through which the tube is inserted. If the auricle be now opened, the ventricle is found cut off from view by a tense membranous parachute-like dome, convex towards the auricle, which is the mitral valve in position; not a drop of water will escape from the ventricle, though the heart be turned upside down, and it requires some little force to depress the valve.

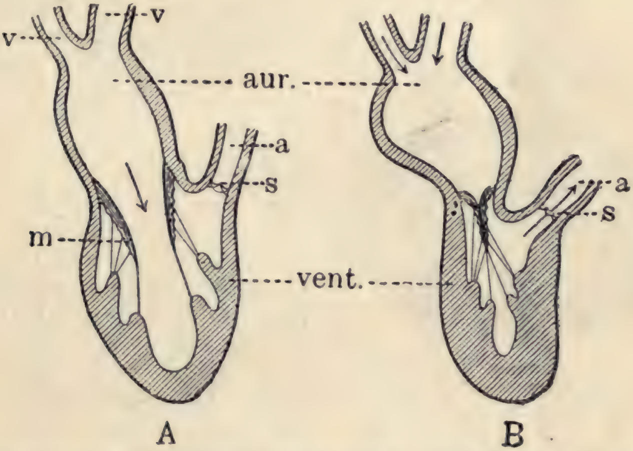

FIG. 15.—DIAGRAM TO ILLUSTRATE THE ACTION OF THE VALVES OF THE HEART (HUXLEY).

In A the auricle is contracting, ventricle dilated, mitral valve open, semilunar valves closed. In B the auricle is dilated, ventricle contracting, mitral valve closed, semilunar valves open. *Aur.*, auricle; *vent.*, ventricle; *v.*, *v.*, vein; *a.*, aorta; *m.*, mitral valve; *s.*, semilunar valve. Note the manner in which the papillæ have shortened in B, in order to compensate for the approximation of the ventricular walls to the surfaces of the mitral valve.

During the filling of the ventricle the auriculo-ventricular valves are coming into position; the blood is under them, and the final systole of the auricle, by raising the pressure in the ventricles, forces these valves into their place, and bulges them upwards towards the auricular cavity. We have seen that even in the dead heart their fit is so perfect that they render the ventricle water-tight. But in the living heart the walls of the ventricles are approximating as they contract on their contents, and though the internal diameter is being reduced in every direction, this does not disturb the accuracy with which the valves apply themselves to each other. The papillary muscles compensate for the approximation of the ventricular walls by constantly shortening, and through the *chordæ tendineæ* maintain the segments of the valves in apposition and prevent further encroachment on the auricle.

The semilunar or sigmoid valves, which guard the entrance of the aorta and pulmonary artery, are composed of fibrous tissue, and possess at the centre of each segment a small hard body, the *corpus Arantii*, which is particularly well marked in the aortic valves. It is generally supposed that these shot-like bodies complete the central sealing when the valves are closed, but this view causes too little attention to be paid to the fact that the valves not only meet at their free border, but overlap. Chauveau, with his finger in the pulmonary artery of the horse, states that he has tried to hold back one flap in order to render the opening patent, but the two remaining segments applied themselves so closely to his finger that the orifice was closed. That these bodies are an additional help to the completely tight closing of the valves is undoubted, but the overlapping of the valves is the most important factor.

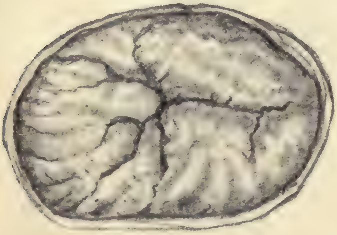

FIG. 16.—TRICUSPID VALVE OF THE HORSE IN CLOSED POSITION SEEN FROM THE AURICLE.

Note the cracks in the surface, which represent where the margin of the valves meet, and fold in against each other like the lips of a toothless mouth.

When the sigmoid valves are not in action, they still lie in the blood-stream, and not against the wall of the vessels, as was at one time supposed, nor do those in the aorta cover the opening of the coronary arteries. It is probable that the valves are enabled to stand out in the blood-stream through the action of vortex currents, and while thus waiting for their turn in the heart's cycle they form a triangular orifice with curved sides.

It is generally believed that both the aortic and pulmonary valves are closed by the regurgitation of the blood ; but it has been pointed out that as the blood is leaving both ventricles, it is streaming through orifices which at that time are mere chinks, owing to the pads of heart muscle which take their origin from all sides of the mouth of the vessels. Vortices are thus created in the space between the arterial root and the edge of the valves. These vortices tend to press the edges of the valves together, and the valves consequently close the moment the blood actually ceases to stream through the narrow crevice. In this way there is no regurgitation, as the valves are closed before the recoil of the aorta. If this explanation be correct, the second sound of the heart must be considered as due to the sudden *tension*, and not the closure, of the aortic valves at the time of the aortic recoil.

It is of the utmost importance to bear in mind that the force of the aortic reflex is not wholly expended on the valves, but largely on the muscular tissue of the ventricle, which here, as the result of the orifice contracting, forms a large circular pad. In order to admit of this strain coming on the heart wall itself, the diameter of the aorta is much greater than the opening out of the ventricle.

Movements of the Heart.—If the exposed mammalian heart be watched at work, a great deal may be learnt of its action. It will be observed that both auricles contract together and both ventricles together ; further, that certain changes in shape occur. The contraction of either auricle or ventricle is spoken of as its **systole**, while the subsequent relaxation is described as its **diastole.** The contraction of the ventricles is succeeded by a *pause*, during which the heart is in a state of relaxation.

A **Cardiac Cycle** is the term used to describe the changes which occur in the heart during the time which elapses between one contraction or relaxation of the auricle, and the one which immediately succeeds it.

We may take the moment when the blood is entering the auricles from the venæ cavæ and pulmonary veins as the most convenient point to start from. This flow is brought about by the pressure of blood in the veins, which, though low, is yet higher than that in the auricles. The influence of gravity is also a great aid to filling the auricles, for, speaking broadly, excepting in the limbs, the bulk of the veins in the body of quadrupeds are above the heart. The emptying of the anterior and posterior vena cava is largely assisted by gravity ; even in the latter there is a downward incline in the vessel from the last valves met with in the iliac veins to the right auricle. Besides this factor there is the contraction of the abdominal wall and consequent pressure on the viscera, so that at each expiration the blood is spurted along the posterior vena cava towards the auricle. Finally, there is an aspiration in the veins produced by the auricle, and caused by a relaxation of its walls after the previous contraction. There is also an aspiration in the thorax, the result of inspiration, which produces a negative pressure in the veins leading to the heart, and so draws blood towards the heart from the veins lying outside the thorax.

By a combination of these means the auricles are filled with blood, and a wave of contraction which first appears at the vessels leading into them passes over the chambers ; the auricular appendage becomes pale, the auriculo - ventricular groove is drawn upwards, and the auricles, by a sudden sharp and brief contraction, empty their contents into the ventricle. At this moment a backward positive wave is produced in the anterior vena cava, which shows itself by a pulsation in the jugular veins at the root of the neck, well seen in the horse.

The effect of the auricular contraction is to complete the filling of the ventricles and close the valves by raising the pressure in those cavities. During the whole time the valves are open the ventricle is filling ; what the systole of the auricle effects is the final filling of the ventricle. The auriculo-ventricular valves, which during the filling have been gradually passing into position, are now, under the sudden increase of intraventricular pressure, rapidly closed, and bulge into the auricle, their closure producing the first sound of the heart. The valves are prevented from going too far by the *chordæ tendineæ*, which are acted upon by the gradually contracting *musculi papillares*, as previously explained. At this moment the blood imprisoned in the ventricles is shut off from the auricles by the closed auriculo-ventricular valves, and shut off from the aorta and pulmonary artery by the closed semilunar valves. The ventricles now contract and raise the pressure within their cavities in order to force open the semilunar valves, for until the pressure within the ventricle exceeds that in the aorta and pulmonary artery, these two avenues of escape are closed. While the intraventricular pressure is being increased by the walls contracting tighter and tighter on the imprisoned blood, the heart is changing in shape ; it is becoming more globular, its walls are growing tenser, it is shortening from base to apex, and in its writhing, screwing efforts to overcome the pressure in the aorta and pulmonary artery it is twisting slightly from left to right, and from before backwards, rotating on its vertical axis, and so brings more of the left ventricle against the sides of the chest. The intraventricular pressure is now sufficient to cause the aortic and pulmonary valves to yield, and blood rushes into these vessels under the systole of the ventricles. The aorta and pulmonary artery fill with blood, elongate and curve ; the heart rotating so long as the ventricles are contracting makes its impulse against the chest wall, and empties its contents into the arteries. The auriculo-ventricular groove now moves downward towards the apex of the heart, the ventricular walls relax and elongate, the pressure within them falls, and the blood from the over-full arteries is prevented from regurgitating into the ventricles by the semilunar valves coming into position, and the closure of these valves creates the second sound of the heart.

The ventricles are at this stage momentarily isolated, the auriculo-ventricular valves are closed, so also are the semilunar. This is the second time in the cardiac cycle that the ventricles have been shown to be cut off from the other part of the heart. We shall examine the question in greater detail presently. The great arteries now contract and shorten, the heart rotates backwards to the left, the auriculo-ventricular valves open, the auricles and ventricles, neither contracting nor dilating, assume a passive condition during a period known as the **pause**, the blood flows into the auricles, and from the auricles into the ventricles; the auricles now contract, and the whole process is repeated.

We have thus the contraction of the auricles, the contraction of the ventricles, and the pause. The time that each of these occupies has not been determined with accuracy; the results obtained by Chauveau and Marey on the horse show that the auricular systole is brief, the ventricular systole twice as long, and the pause equals in length the ventricular systole; but the time values as given by them would cause the horse to have a pulse-rate of 60, which is abnormal. From 36 to 40 beats per minute is the normal rate, and this gives a period of 1·5 seconds for a complete cycle of the heart.

There is a well-marked interval between the contraction of the auricles and that of the ventricles, during which not only is the ventricle getting up pressure, but the papillary muscles are contracting to prevent the valves being pressed up further into the auricles. Chauveau draws especial attention to the interval in the horse which has been named the **intersystolic period.** It must not, of course, be confused with the pause of the heart which follows ventricular systole. The auricles have a longer period of rest than the ventricles, but, as we shall see later, they are not entirely idle between each systole. One important point may here be conveniently stated, that no matter how fast the heart is beating, the frequency depends, not on the duration of the ventricular systole, but on the length of the subsequent pause.

Summary of Events occurring during a Cardiac Cycle.—Dividing the events into three periods, and starting with the contraction of the auricles, the following is a summary of the changes occurring in the heart:

First Period.—The contraction of the auricles completes the filling of the ventricles.

Second Period.—The auriculo-ventricular valves are closed, the ventricles contract, the aortic and pulmonary valves open, blood is pumped into the aorta and pulmonary artery, the impulse of the heart is made against the wall of the chest, the first sound is produced, the auricles fill with blood, and the whole is followed by a short pause.

Third Period.—The aortic and pulmonary valves close, the second sound of the heart is produced, followed by a long pause, during which diastole of both auricles and ventricles occurs, the auriculo-ventricular valves open, and blood flows into all the chambers.

The impulse of the heart, to which we have previously referred as being felt externally between the fifth and sixth ribs, is not given by the apex, but by the lower half of the left ventricle. There is no such thing as an apex-beat ; the apex practically does not move as long as the heart is retained within the pericardium, but if the latter be opened, the apex is tilted forward with each contraction. The **Use of the Pericardium** is to prevent over-distension of the heart.

Cardiac Sounds.—There are four sources of sound in the heart, but as they work in pairs only two sounds are heard. We have previously indicated where these occur in the heart's cycle. The *first sound* is a long, booming one, and is made up of two causes—the muscle sound of the contracting ventricle and the closure of the auriculo-ventricular valves. The proof that the valves are not wholly responsible for the first sound is that the bloodless, beating heart still gives out a sound during ventricular systole.

The cause of the *second sound* has never been doubted ; it is due to the closure of the aortic and pulmonary valves ; it may be abolished by hooking these back, and re-established by releasing them. Under pathological conditions when the aortic valve is destroyed a murmur takes the place of the normal heart sound. When an animal is bled to death the second sound disappears before the first—in fact, it is abolished immediately the amount of blood propelled into the aorta is insufficient to distend this vessel properly.

As the first sound of the heart is heard just before the systole of the ventricle, it is termed the 'systolic'; while the second sound, occurring at the beginning of diastole, is termed the 'diastolic.' On auscultation the two sounds are heard with unequal intensity at different parts of the cardiac area. They are heard better on the left side than the right, not because the heart is nearer to that side than to the other, but for the reason that there is a larger gap in the left lung, which exposes the heart and allows its impulse to be felt against the chest wall. The two sounds are very accurately represented by the words *lŭb dŭp*.

Intracardiac Pressure. — Most important additions to the physiology of the heart have been made by studying the pressure existing in its chambers. The pressure exerted upon the blood by the heart varies from moment to moment ; the pump is for ever being charged and discharged, and both these processes depend upon the condition of internal pressure existing at the time. An examination of this internal pressure not only throws light upon the circulation, but also furnishes a better understanding of the mechanism of the heart itself.

It is interesting to note that the first experimental work done in this connection was carried out by a French veterinary surgeon, Chauveau, in conjunction with a physicist, Marey. Their work, for beauty, originality, and exactitude, has only recently been exceeded. Observations were made on the horse by means of an instrument known as the *cardiac sound*, a diagram of which may be seen in Fig. 17. It is a double tube, having at its extremity two elastic balls separated so that when the apparatus is introduced into the heart, on the right side through the jugular vein, and on the left through the carotid artery, in each case one ball lies in the auricle and one in the ventricle. The air in the apparatus is compressed when the heart's cavities contract, and the compression moves a lever placed in connection with a recording surface. The introduction of the apparatus causes no pain, and as there are no sensory nerves in the lining membranes of the bloodvessels or heart, its presence gives rise to no inconvenience. Chauveau, in one of his memoirs, states that the pulse-rate was not disturbed, and the introduction of the instrument did not cause the animal to cease feeding.

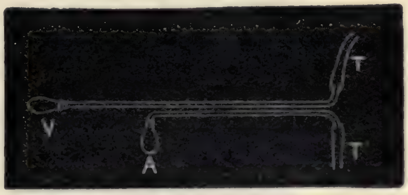

FIG. 17.—DIAGRAM OF CARDIAC SOUND.

A, Elastic ampulla for auricle; V, for ventricle. T, tubes connected with recording tambours.

A tracing taken by means of the apparatus just described is seen in Fig. 18. In it may be seen a curve obtained simultaneously from the auricle and ventricle; the vertical dotted lines indicate coincident periods in both chambers. Taking the auricular curve, there is a sharp, sudden rise, indicating auricular systole, followed by a sudden fall in pressure, and the contents of the chamber are discharged. This is succeeded by two minor rises and falls in pressure before the pause in the heart's cycle D is reached. The curve of intraventricular pressure shows a slight and temporary rise at the moment the auricle reaches its maximum of pressure, and immediately afterwards a sharp, sudden rise in the intraventricular pressure starts. The pressure is maintained for a short time when once it has reached its maximum, and the curve is in consequence flattened; this flattening is called the *systolic plateau*, and is followed by an abrupt fall the moment the pressure within the ventricles is sufficiently low to allow the aortic and pulmonary valves to close. The fall in pressure which represents the end of the ventricular systole is followed by the pause D, and this is once more succeeded by a contraction of the auricles.

All that we have attempted to do in the above is to focus attention on the fact that certain positive and negative waves of pressure are constantly occurring in both chambers of the heart. Their shape on a recording surface depends upon the nature of the apparatus employed ; their significance remains, and must now engage our attention.

There are three 'standard movements' in the heart to which other cardiac events may be referred in point of time ; in the measurement and interpretation of pulse tracings in clinical work these are important landmarks. One is the *closure* of the semilunar valves of the aorta and pulmonary artery, another is the *opening* of the auriculo-ventricular valves. The first is known for brevity as the 'S.C. period,' the second is known as the 'A.O. period.'

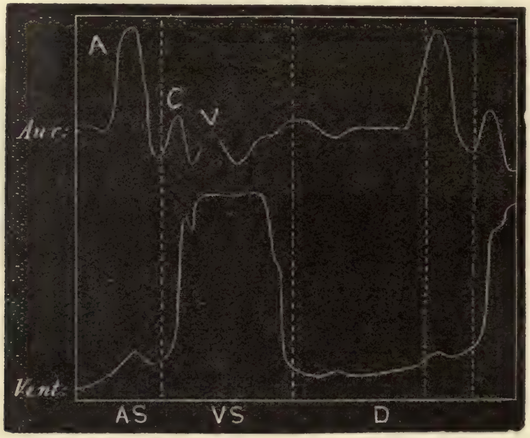

FIG. 18.—CURVES OF ENDOCARDIAC PRESSURE TAKEN WITH CARDIAC SOUNDS.

Aur., Auricular curve ; *Vent.*, ventricular curve ; AS, period of auricular systole, including relaxation ; VS, of ventricular systole, including relaxation ; D, pause.

In Fig. 18 the S.C. period occurs near the end of the ventricular plateau, just when the pressure in the ventricle becomes less than that in the aorta and pulmonary artery ; the A.O. period occurs at the bottom of the down-stroke. Between these two points, brief as it is, matters within the heart are in rather a peculiar condition : the semilunar valves are closed, but the pressure in the ventricles is still too high to admit of the auriculo-ventricular valves opening, so that for this brief period no blood is entering the ventricles, which are screened off from all parts of the circulatory system. This period is known as the *postsphygmic*. Meanwhile the ventricular walls are relaxing, and as the cavity of the ventricle expands the pressure falls sufficiently to allow the auriculo-ventricular valves to open, and blood pours in from the auricle.

This is now the period of heart pause, during which both auricles and ventricles are filling simultaneously; it is succeeded by the contraction of the auricles, by which the ventricles are still further distended, and under the steadily increasing pressure in the ventricles the auriculo-ventricular valves are closed. This point occurs in Fig. 18 shortly after the beginning of the up-stroke on the ventricular curve. The closure of the auriculo-ventricular valves is referred to as the *third standard movement*. The ventricles are now full of blood shut off from the auricles by the auriculo-ventricular valves, and shut off from the general circulation by the closed aortic and pulmonary valves. This period, which is extremely brief, is known as the *presphygmic*, the period of rising pressure, or, as Stewart graphically puts it, the period during which the ventricles are 'getting up steam.' No blood can leave the ventricles until the pressure in their cavities rises above the aortic and pulmonary pressures. With the opening of the semilunar valves the blood is leaving the heart, and it continues to leave it during the period shown on the tracing as the systolic plateau.

If Fig. 18 be again referred to, and the curve given by the auricles examined, three well-marked waves will be seen; the first and largest, known as 'A,' we have previously referred to as corresponding with the contraction of the auricle; the second positive wave, known as 'C,' occurs during the rising pressure in the ventricles, and is probably due to the bulging of the auriculo-ventricular valves into the interior of the auricle. Chauveau, with a finger in the contracting auricle of the horse, says this upward bulging does occur. The cause of the third wave, known as 'V,' is not yet agreed upon. The interest in these auricular curves is mainly clinical; similar waves may be observed in veins near the heart, and the venous pulse thus obtained may be employed to indicate irregularities in auricular contraction. We shall see presently that the contraction of the heart is initiated in the right auricle, so that a clinical examination of the behaviour of this cavity through the medium of the jugular pulse is a method of diagnosis of the utmost importance. In modern investigations of heart irregularities the most valuable information is being afforded by the A to C interval, or the time distance between the waves representing auricular and ventricular systole. In Fig. 19 may be seen a venous pulse-tracing from the dog in relation to auricular and ventricular contraction. The information thus obtained regarding the condition of the auricle is comparable with that obtained by the cardiograph and pulse-tracing in relation to the condition of the ventricle.

Intracardiac Pressures.—The positive and negative pressures in the heart in large dogs have been measured with the following results:

Right auricle: maximum positive, 20 mm. (¾ inch) of mercury; minimum negative, –10 mm. (½ inch).
Left ventricle: maximum positive, 230 to 240 mm. (9¼ to 9½ inches); minimum negative, –30 to 50 mm. (1¼ to 2 inches).
Right ventricle: maximum positive, 70 mm. (2¾ inches); minimum negative, –25 mm. (1 inch).

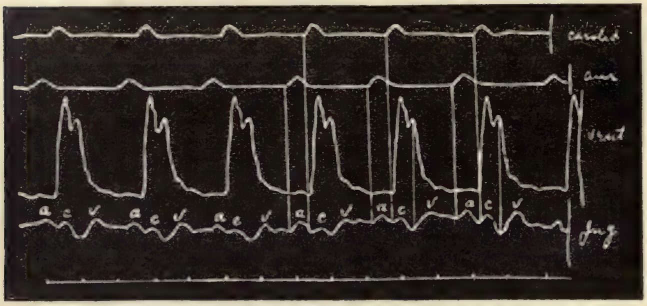

FIG. 19.—SIMULTANEOUS RECORD OF JUGULAR PULSE, VENTRICULAR CONTRACTION, AURICULAR CONTRACTION, AND CAROTID PULSE, IN THE DOG (CUSHNY AND GROSH).

a, c, v, the three elevations of the jugular pulse. (Time-trace, fifths of a second.)

In the horse the maximum pressure in the left ventricle has been found to be from 178 to 318 mm. of mercury (7¼ to 12¾ inches), or a column of blood 2·4 to 4·3 metres (9 to 14 feet) in height. In the right ventricle of the same animal the maximum pressure was 34 mm. (1½ inches), equal to a column of blood 0·46 metre (1½ feet) high.

The negative pressure within the heart has not been satisfactorily explained. According to one view, the heart behaves like the bulb of a flexible syringe, which is discharged by pressure and filled by the elastic dilatation of its own walls; but there are objections to this view, inasmuch as no elastic dilatation can be demonstrated by experiment, nor have any of the other views put forward been supplied by conclusive experimental evidence. The explanation that the dilatation was due to the aspiratory effect of the air-tight thorax may be negatived by the fact that the negative pressure may be still recorded with the thorax open. In fact, the explanation of cardiac dilatation has yet to be found.

The **Cardiac Impulse** has been studied by means of an instrument termed a *cardiograph*, which transmits the impulse of the heart on the chest wall to a recording apparatus. Curves so obtained are often difficult to interpret; they are the graphic record, not of one, but of a series of events, the chief of which are variations in ventricular pressure and changes in volume. In Fig. 20 is a cardiogram which shows a small elevation corresponding to auricular contraction, followed by a large rise due to ventricular systole, with a sudden and then prolonged drop indicating relaxation of the ventricles. In the horse the impulse of the heart occurs on the cartilages of the fifth and sixth ribs, close to the articulation with the rib, the centre of the shock being the fifth intercostal space (see Fig. 45, p. 105).

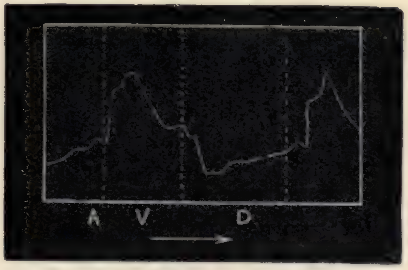

FIG. 20.—CARDIOGRAM TAKEN WITH MAREY'S CARDIOGRAPH (STEWART).

A, Auricular systole; V, ventricular systole; D, diastole. The arrow shows the direction in which the tracing is to be read.

The Capacity of the Heart may be ascertained by enclosing it in a chamber termed a *cardiometer*, and measuring the change of volume during systole and diastole.

Observations so conducted show that the ventricle does not empty itself at each systole; as much as one-third of the blood may be left in it. Colin, many years ago, showed the same thing for the horse, and stated that not more than two-thirds or three-fourths of the ventricular charge was expelled. The quantity of blood which the heart is capable of dealing with cannot be ascertained by measuring the capacity of the chambers. Munk gives the capacity of the horse's ventricle at 1 litre (1·76 pints), equivalent, roughly, to 1 kilogramme (2·25 pounds) blood, and states that each ventricle contains one-thirtieth of the blood in the body, so that when both contract one-fifteenth of the total blood is ejected. Both ventricles deliver the same amount of blood, for there is as much entering the heart as there is leaving it.

Work of the Heart.—This may be calculated if we know the amount of blood being discharged from the heart at each stroke, and the pressure against which it is propelled. The amount pumped out at each systole of the ventricle is liable to great variation; at least, such are the results of experiments on the dog, in which animal it has been shown that the contraction volume of the left ventricle diminishes as the size of the animal increases. It is obvious that the right ventricle does less work than the left, for the reason that it has to pump the same volume of blood against a much smaller *peripheral resistance;* it has been said, indeed, that the right heart does one-quarter the work of the left. Colin placed the impulsive force of the right ventricle of the horse at 33 kilogrammes (72·6 pounds), and of the left at 132 kilogrammes (290·4 pounds).

If we take the amount of blood pumped at each stroke into the aorta of the horse as about 1 kilogramme (2·25 pounds) in weight, and the pressure under which it is forced upwards as equivalent to a column of blood 3·048 metres (10 feet) in height, then the work of the left ventricle at each stroke is equal to 10 kilogrammes (22·5 pounds) raised 0·304 metre (1 foot) high, or for twenty-four hours, allowing the work of the right heart to be one-fourth that of the left, 212,275·86 kilogramme-metres (1,539,000 foot pounds). This amounts to about one-thirtieth of a horse-power per diem; Munk places it at one-thirty-sixth of a horse-power. If the amount of blood expelled by the left ventricle at each stroke be equal to 1 kilogramme, then in a state of repose the entire blood in the body of a horse passes through the heart in about thirty beats, or in forty-five seconds. Munk says that in the horse the entire blood passes through the heart in fifty seconds, in the ox in forty seconds, and in the dog in twenty seconds. Since the amount of work performed by the heart is increased during exercise, the above calculations are for a horse in a state of repose.

Coronary Circulation.—The vascular system which supplies the heart substance is lodged in grooves in its wall, and much discussion has arisen, not only as to the moment at which the arteries receive their supply, but also as to the effect on the coronary bloodvessels of the contraction of the surrounding heart muscle. It is now generally admitted that the coronary arteries receive their blood during the ventricular systole, and not, as was originally thought, during the closure of the aortic valves. The latter, as we have seen, do not cover the openings of the coronary arteries. The question of the effect of the heart's contraction on the vessels lodged in its walls is far more difficult of solution. If the squeezing of the heart will assist the passage of blood in one direction it must retard it in another, for the veins and arteries lie side by side, and their blood is flowing in opposite directions; the effect on the thick-walled arteries is, however, less than on the thin-walled veins. When the ventricle begins to contract, it can be shown that the pressure and velocity in the coronary arteries is increased; but as the contraction proceeds, and the muscle, as it were, is being wrung, the coronary vessels are clamped, and the blood in the arteries is driven back on the aorta, while that in the veins is forced onwards to the right auricle. At diastole the coronary arteries at once refill, and, as we have seen above, a further charge is pumped in at the beginning of contraction. Other experiments appear to show that with each systole of the heart the coronary system is emptied towards the venous side, and at each diastole it is filled.

The effect of occluding the coronary arteries is of the utmost practical interest. If all the arteries be clamped the heart at once stops; but if the observation be limited to one vessel only, that portion of the ventricle supplied by it ceases to beat. The arrest of the ventricle is a curious condition, giving rise either at once or soon after to the phenomenon known as **fibrillar contraction,** in which the surface of the heart presents vibrating, twitching, disorderly movements, to which the term *delirium cordis* has aptly been applied. It is as if each fibre of the heart were irregularly contracting on its own account, independently of its neighbours.

Fibrillation of the auricles may also be experimentally produced, but the auricles, unlike the ventricles, appear to possess a greater capacity for returning to co-ordinate contraction. Considerable attention is now being paid clinically to fibrillation of the auricles, which Lewis* finds is the commonest persistent irregularity exhibited by the human heart, constituting approximately 50 per cent. of all such cases. He has also observed it in the horse, and it is quite likely that it may turn out to be a relatively frequent condition. Though fibrillation of the ventricles means immediate death, fibrillation of the auricles does not. The ventricles are indispensable to the circulation, but the auricles, as we have seen, are practically reservoirs, and without their assistance the ventricles fill by gravity; in fact, as we have already learnt, under normal conditions the ventricle is nearly full before the auricular systole occurs. Fibrillation of the auricles gives rise to a train of symptoms, sometimes associated with great distress, but not necessarily fatal to life. The cause of this condition will be explained presently.

The Cause of the Heart-Beat.—It seems incredible that the use of the heart should have remained unknown until the early part of the seventeenth century. Even now some of the chief features in its working are obscure, and around one of them, the cause of the heart-beat, much difference of opinion exists.

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* T. Lewis, M.D., D.Sc., 'Auricular Fibrillation,' *Heart*, vol. i., No. 4, 1910.

An ordinary skeletal muscle is under the control of the nervous system by which its movements are carried out, but the hollow heart muscle, whose never-ceasing action is maintained for years with perfect regularity, is known to beat independently of any nervous supply. The evidence of this is conclusive; both the heart of the frog and of mammalia is capable under similar conditions of contracting rhythmically for hours, even for days, when entirely removed from the body, and therefore when no longer in connection with the nervous system. The discovery of nervous bodies called 'ganglia' in the substance of the heart wall at once appeared to afford a solution of the vexed problem of why the heart was capable of spontaneous movements, but it was shown that the embryonic heart was capable of spontaneous movement before any sign of ganglia appeared in its walls. The position in which the case stands to-day is practically represented by the above; physiologists are not agreed as to whether the heart muscle, independently of its ganglia, sets up its own movements, or whether these are initiated by the nervous elements embedded in its walls. The former is called the *myogenic*, the latter the *neurogenic*, theory. Both these views must be briefly examined.

The Neurogenic Theory.—In the walls of the frog's heart, and that of a few other cold-blooded animals, intrinsic nerve ganglia have been discovered, and from this it has been argued that some such arrangement exists in the heart of mammalia. Such, however, has never been demonstrated beyond doubt. Three intrinsic ganglia, known after their discoverers as Remak's, Bidder's, and Von Bezold's, are situated mainly in the venous end of the heart—viz., in the auricles, the junction of auricle and ventricle, and in the interauricular septum. Ganglia have been described as occurring in the ventricles, but at present no conclusive evidence has been brought forward to prove this point.

The neurogenic theory requires that in these ganglia, situated, it will be observed, at that end of the heart which initiates the contraction, impulses are originated which pass out to the neighbouring muscular tissue, and give rise to a regular sequence of events. But there is no evidence in vertebrates that the heart possesses an exclusive motor nervous system charged with the spontaneous production of rhythmical contractions. The whole of the nerves in a strip of heart wall may be cut without the tissue losing its property of spontaneous contraction.

The *myogenic theory* demands that the heart muscle, independent of any nervous supply, shall possess the power of contracting automatically and rhythmically, and the experiment last named lends considerable support to this theory. The contraction of the heart from base to apex is provided for by the A.V. bundle of conducting muscular tissue described at p. 12, which links up auricle and ventricle, while the base of the heart is provided with muscle more pronouncedly automatic than that found in the ventricles, which thus insures the normal sequence of events from base to apex.

Within the right auricle, below and to the right of the coronary sinus, lies the auriculo-ventricular node (Fig. 12), the commencing portion of the A.V. bundle; if this connection be cut or compressed, disturbance of conduction follows known as **heart-block.**

In a work of this kind it is not necessary to enter deeply into vexed questions such as the one we are here considering, but two more points in favour of the muscular theory of contraction may be briefly mentioned.

The normal direction of the wave of contraction of the heart muscle from auricle to ventricle may, under certain conditions, be reversed—viz., from ventricle to auricle. For example, if a ligature be passed around the heart of the frog between the sinus and the auricle (Stannius's experiment), the auricle and ventricle cease to beat; if now the ventricle be stimulated to contract, the auricle follows. On the theory of muscle conduction this experiment can be explained, but not on that of nerve conduction.

The balance of evidence is in favour of Gaskell's myogenic path as the conducting medium of automatic action, but this still leaves the question of the nature of heart automaticity untouched.

Heart Automaticity.—A heart, even one which has been apparently dead for some time, may be revived by placing it in an atmosphere of oxygen and transfusing through its vessels a solution containing sodium, calcium, and potassium chloride, sodium carbonate, and grape-sugar. It was Ringer who was the first to show that a fluid containing sodium, potassium, and calcium chloride of a definite strength would keep the frog's heart beating for days; but it is only recently that the mammalian heart, and one even that has been apparently dead some days, has been shown to be capable of resuscitation. Sodium, potassium, and calcium chloride are not only required of a definite strength, but practically no substitute is efficient. The dextrose and sodium carbonate are added to increase the effectiveness of the work, but they are not essential; on a diet of inorganic salts the heart is capable of beating rhythmically for days.

We have at p. 6 referred to the action of a 0·9 per cent. solution of sodium chloride as a physiological solution. It is sodium chloride which, in a strength of 0·5 to 0·6 per cent., is mainly responsible for the normal osmotic pressure of the blood, and though single-handed it is not capable of maintaining the heart-beat, nor of furnishing the tissues with all the inorganic material they require, nevertheless it is more effective in this respect than any other single salt. The presence of calcium, though the amount in blood is only small, appears to be necessary to contraction ; at any rate, the addition of calcium to the 'fed' heart, or its application to the isolated strip, not only brings on contractions, but increases the length of time during which they are continued. The physiological effect of potassium appears to be connected with relaxation rather than with contraction.

Facts such as the above suggest that the heart is capable of generating in its own substance a stimulus to contraction, and the hypothesis of an *inner stimulus*, though it takes us no nearer to a conception of its nature, assists the imagination. It is not considered that the inner stimulus is represented by the inorganic salts, but rather that in the presence of these it is capable of doing its work.

The Physiological Properties of Cardiac Muscle differ from those of skeletal muscle. The stimulation of skeletal muscle with a weak current causes a weak contraction, with a strong current a more powerful contraction ; but the heart muscle behaves differently : the amount of contraction it exhibits under stimulation is the full amount which it is at the time capable of exhibiting, no matter whether the current be a weak or a strong one. This remarkable difference has been explained by the fact that in skeletal muscle the fibres are isolated from each other, while in heart muscle they form a continuous sheet, and the excitation travels from fibre to fibre.

Another distinction from skeletal muscle is the reaction to repeated electrical stimulation. If a rapid series of induction shocks be passed into skeletal muscle, it is thrown into a condition known as *tetanus ;* but heart muscle cannot be tetanised, for the reason that electrical stimuli applied to it during the period of its contraction produce no effect whatever. It is only during diastole that a response to stimulation is obtained.

The non-irritable nature of the heart muscle during its contraction is spoken of as the **refractory period**, and the response to stimulation applied during diastole is described as an **extra contraction**. Having executed this contraction out of its regular sequence, the succeeding pause is longer than usual, by which means the heart picks up its rhythm as though it had never been disturbed. The pause is known as a **compensating pause.**

The heart muscle stands by itself in being non-irritable during its period of actual contraction ; neither skeletal nor plain muscle exhibit this phenomenon. The refractory period is in all probability connected with the internal metabolic processes concerned in the building up of the heart's contractile material, and it appears at present impossible to separate it from the fundamental processes of rhythmicity.

The direction of a contraction through the mammalian heart is from auricles to ventricles via the auriculo-ventricular bundle ; the rate of conduction through this bundle is slower than that through the ordinary heart muscle, which explains the slight pause between the contraction of the auricles and that of the ventricles. The rhythm set by the auricles is under normal conditions taken up by the ventricles ; but experimentally it can be shown that interference with the A.V. bundle may lead to the rhythm of the ventricles being slower and independent of that of the auricles. The precise results obtained depend upon whether there is a partial or complete **block** between the auricles and ventricles. The condition thus experimentally produced has its clinical counterpart in irregularities due to heart-block.

One word more may be said in connection with the transmission of a contraction through the heart. Chauveau has shown that the two auricles in the horse do not contract precisely together ; there is a slight delay in the contraction of the left, and this is explained by saying that the transmission of the contraction from right auricle to left auricle takes time.

Nervous Mechanism of the Heart.—Up to this point the question of the rhythmical contraction of the heart has been considered ; we have now to take up another and distinct question—viz., the influence of the nervous system in regulating the activity of the heart. The heart receives a nerve supply from two portions of the central nervous system : one is concerned with the transmission of impulses which slow or stop the heart, hence called *inhibitory ;* the other conveys to the heart impulses which stimulate or augment the activity, and are in consequence known as *augmentor* or *accelerator* nerves. From the **vagus** is derived the inhibitory effects, and from the **sympathetic** the augmentor. It is obvious that these nerves are antagonistic, the one endeavouring to slow the heart, the other pressing it on. The balance between these two opposite conditions results in the normal rate of heart-beat.

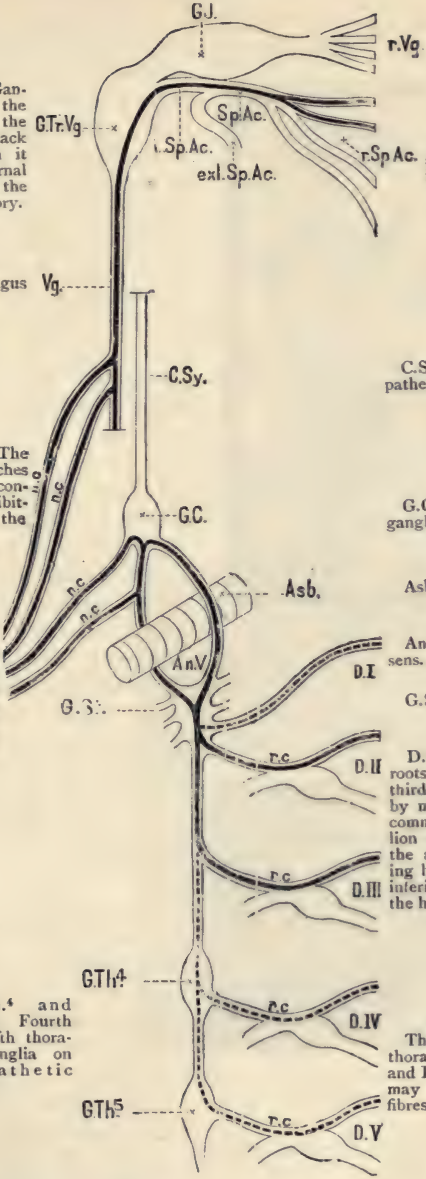
Not only have these two nerves opposite functions, but they are also structurally different, the vagus being a medullated, the sympathetic a non-medullated nerve.

An immense amount of work has been done in endeavouring to elucidate the physiological effect of the vagus and sympathetic on the heart, and the results have not always been concordant. This may be due to the fact that the frog has furnished the bulk of the experimental material. The physiology of this creature's heart is known more completely than that of any other animal, but what is known cannot always be applied to the mammal, owing to anatomical differences in the arrangements of the nerve.

In the frog there is a vago-sympathetic nerve in the neck, in which the fibres of both nerves are anatomically mixed, though functionally distinct; the mixing up does not occur in the chest, as in the mammal, but close under the skull. When this vago-sympathetic is stimulated, either inhibitory or augmentor effects may be obtained, according as to which one of the set of nerve-fibres in the mixed nerve happens to be most efficiently stimulated. The mixing of the fibres takes place in the ganglion of the vagus nerve, which lies just outside the skull. If the intracranial fibres of the vagus are stimulated, the effect on the heart is purely inhibitory, and if the fibres of the sympathetic are stimulated just before they enter the ganglion, the effect is entirely augmentor. In the mammal the vagus and sympathetic are distinct, even if, as in some animals, they run in the same sheath; while accelerator fibres do not join the sympathetic until it enters the thorax.

In the mammal the vagus arises from the medulla; the inhibitory fibres it receives are derived from the spinal accessory and join the vagus within the skull; the cardiac branches of this nerve are given off from it in the thorax. The sympathetic supply to the heart comes out of the spinal cord at the second and third dorsal nerves, probably others, and by means of the *rami communicantes* passes to the stellate ganglion, thence to the inferior cervical ganglion on the cervical sympathetic trunk, and from this ganglion they pass to the heart. The above arrangement applies especially to the dog, and is shown diagrammatically in Fig. 21; it is not quite the same for all mammals. The rich plexus of nerves on the surface of the horse's heart may be seen in Fig. 22, and that of the calf in Fig. 23.

Function of the Vagus.—If the vagus in the neck be cut and its peripheral end stimulated, the rate of the heart-beat is slowed and the force of the beat diminished. If stronger stimulation be applied, the heart stops in a condition of dilatation, and becomes swollen with blood. Slowing of the heart-rate is the most prominent effect of vagus stimulation, and this in the mammal is more apparent in its effect on the auricles than on the ventricles. The strength of the ventricular contraction may continue undiminished at the time the auricles are suffering from inhibition, and should the stimulation be sufficiently strong to cause the auricles to cease contracting, the ventricles for a brief time are inhibited, and then beat again independently. In other words, in the mammal the vagus is essentially an



G.Tr.Vg. Ganglion on the trunk of the vagus; the black line through it is the internal branch of the spinal accessory.

Inhibitory fibres from spinal accessory entering the vagus.

Vg. The vagus nerve.

C.Sy. The cervical sympathetic nerve.

nc., nc. The cardiac branches of the vagus conveying inhibitory fibres to the heart.

G.C. Inferior cervical ganglion.

Asb. Subclavian artery.

An.V. Annulus of Vieussens.

nc., nc. Cardiac branches of the sympathetic conveying augmentor fibres to the heart.

G.St. Ganglion stellatum.

D.II., D.III. The inferior roots of the second and third spinal nerves, passing by means of r.c. the ramus communicans to the ganglion stellatum. These are the augmentor fibres, passing both by the annulus and inferior cervical ganglion to the heart by nc. nc.

G.Th.4 and G.Th.5 Fourth and fifth thoracic ganglia on sympathetic chain.

The dotted line in certain thoracic nerves, D.I., D.IV., and D.V., indicates that they may contribute augmentor fibres to the sympathetic.

FIG. 21.—DIAGRAMMATIC REPRESENTATION OF THE CARDIAC INHIBITORY AND AUGMENTOR FIBRES IN THE DOG (FOSTER).

The upper portion of the figure shows the inhibitory, the lower the augmentor, fibres.

auricular nerve. The phenomenon of inhibition is not shown immediately on the application of the stimulus; there is at least one contraction of the heart before it slows or ceases to beat. This delay is known as the **latent period** (Fig. 24). In some animals, such as the cat, even the stronger stimulation of the vagus only slows the heart; it does not stop it; whereas with the dog relatively weak stimulation may bring the heart to a standstill. Fig. 25 shows the effect on blood-pressure of weak and stronger stimulation of the vagus.

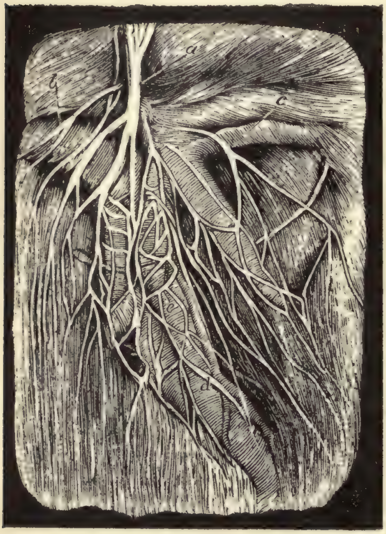


FIG. 22.—NERVES ON THE SURFACE OF THE HORSE'S HEART (PETTIGREW).

a, Nerve descending to the auricle; *b*, *c*, coronary vessels; *e*, *d*, vessels in anterior ventricular furrow.

Inhibition does not last long; it may, of course, cause death, but as a rule it is overcome and the heart starts again. Moderate stimulation of the vagus sufficient to slow the rate may be tolerated for some time. In the frog the same escape from inhibition may be seen. The heart subsequently makes up for lost time by working at a greater rate or strengthening its contractions, until it regains its usual rate of working. When an inhibited heart behaves in this way, it is spoken of as *secondary augmentation*, and the phenomena, though best seen in the frog, may also, though in a less marked degree, be seen in the mammal.

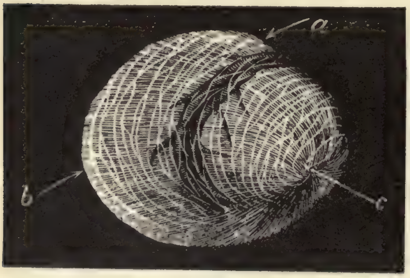
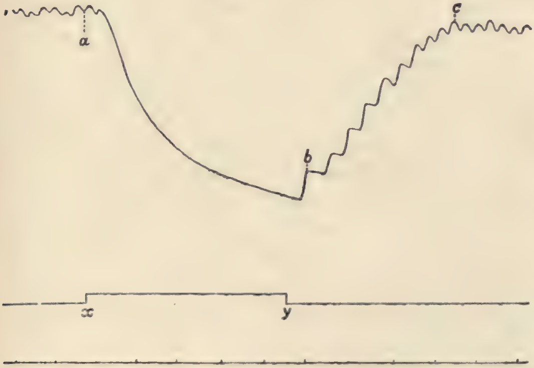


FIG. 23.—NERVES ON THE SURFACE OF THE LEFT VENTRICLE OF THE CALF (PETTIGREW).

The nerves take a spiral direction, like the muscle fibres; *c*, apex of ventricle.

Reflex inhibition of the heart may arise through a sensory surface, as in painful impressions, or a blow on the abdomen, and in other ways. Afferent impulses — that is, impulses conveyed *to* a nerve centre from without — must pass through the centre from which the inhibitory fibres of the heart arise, and though such a centre has not been defined with exactitude, the existence of a *cardio-inhibitory centre* in the medulla is undoubted. From this centre impulses issue which in a normal state throughout the whole life of the animal are passing down the vagus, keeping a constant watch and control over the rate of the heart, and the evidence that such a view is not a fanciful one is shown by the result of cutting off these impulses by dividing both vagi, when the frequency of the heart-beats is greatly increased. This constant action of a nerve centre is known as *tonic activity*, and this in all probability, is the outcome of impulses flowing



x, Marks on the signal line when the current is thrown into, and *y* shut off from the vagus. The time-marker below marks seconds. *a* corresponds in point of time with *x*; the heart does not at once cease to beat. The first beat, *b*, occurs a short time after shutting off the current. The notches in the tracing are due to the beats of the heart.

FIG. 24.—TRACING SHOWING INFLUENCE OF THE ARREST OF THE HEART ON BLOOD-PRESSURE, DUE TO STIMULATING THE VAGUS (FOSTER).

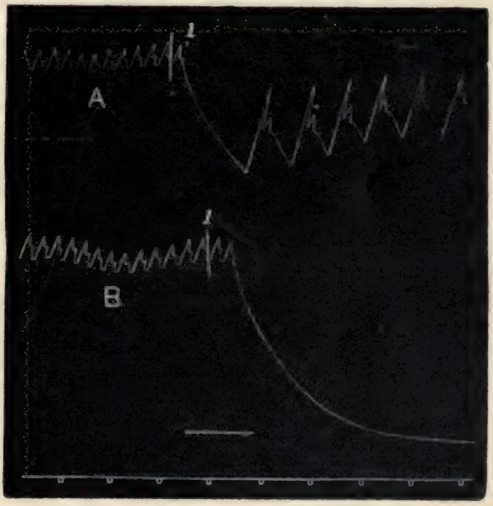


FIG. 25.—BLOOD-PRESSURE TRACINGS: RABBIT (STEWART).

Vagus stimulated at 1; stimulation stronger in B than in A (Hürthle's sphygmanometer).

into it through sensory nerves ; a mechanism so arranged produces what is known as a *reflex tonus.*

The *Action of Poisons on the Heart* has been appealed to in order to decide not only their pharmacological effect, but also as a physiological means of research in connection with its nervous mechanism. *Atropine* causes the heart-rate to become quickened, due to the inhibitory effect of the vagus being suspended. If the vagus under these conditions be stimulated, no inhibition follows, and it is argued that this is due to paralysis of the nerve terminations of the inhibitory fibres in the heart muscle, much as the motor end-plates are in muscles under the action of curare. *Muscarine,* a poison obtained from certain mushrooms, causes the heart to slow down, and finally to stop. *Pilocarpine* has much the same effect, and it is assumed that both these alkaloids stimulate the inhibitory fibres. This view is strengthened by the fact that atropine abolishes the inhibitory effect produced by muscarine and pilocarpine, and it is considered that the result is due to the paralysis of the terminals of the inhibitory fibres in the heart muscle.

Function of the Sympathetic Nerve.—The course of the accelerator fibres derived from the sympathetic has been previously described. Their distribution in the heart is mainly to the ventricles. The vagus fibres, it will be remembered, are principally distributed to the auricles. If the sympathetic trunk in the neck of the mammal be stimulated, no effect follows, for, as Fig. 21 shows, there are no accelerator fibres above the inferior cervical ganglion. If certain branches issuing from this ganglion be stimulated, the heart-beats are increased in frequency, and sometimes, but not always, in force ; in other cases they are increased in force and not in frequency. There is reason to think these differences are explained by the probability that the accelerator fibres consist of two sets, one increasing the frequency of the heart, and the other increasing the force. From either the right or left ganglion accelerator effects can be obtained on stimulation, but the augmentor effect is best obtained from the left side.

The accelerator fibres, like the inhibitory, are in a state of constant or tonic activity, as evidenced by the fact that, if they be divided, the heart-rate is thereby decreased. It has been assumed that this constant activity is carried out by a centre situated in the medulla, and that to it afferent impulses pass of a reflex nature which either increase or decrease its activity. No better example of a reflex stimulation of the accelerator centre could be witnessed than is shown in the fright of a startled nervous horse ; the heart may almost be heard thumping against the chest wall.

No such accelerator centre has actually been located in the medulla, but the probability of its existence is considerable. On the other hand, it is not a physiological necessity ; acceleration might be brought about by inhibition of the cardio-inhibitory centre, and experiment has shown the possibility of the effect being produced through this channel.

The Nature of Inhibition.—The discovery of the inhibitory action of the vagus was a great addition to physiological knowledge ; it settled the important point that such an effect could be produced through the nervous system, and has been the means of adding considerably to the physiological knowledge of other organs besides the heart. The actual means by which inhibition in the heart is brought about is still a matter of speculation ; the view most generally accepted is that propounded by Gaskell. He regards the vagus as the protecting nerve of the heart, and reasoning from the observed fact that after its stimulation and consequent inhibition there is on recovery an improvement in the rate or force of the heart-beats, he concludes that during inhibition there is a building up—*anabolism*—of the muscular tissue which results in the improved condition of the heart. Such changes are of an opposite character to those occurring during contraction, which are of a *katabolic* or tissue-destroying nature, by which complex substances are converted into simpler ones, with the production of heat and energy. The latter changes are regarded as brought about by the sympathetic system. During inhibition the heart is being repaired, during contraction its substance is being used up, and Gaskell believes that all muscular tissue is similarly provided with anabolic and katabolic nerves.

The Depressor Nerve.—The nervous mechanisms considered up to this point are concerned in bringing about some modified action of the heart, under the guiding influence of a nerve centre in the medulla. We have now to consider the case where a nerve running *from the heart* to the medulla is engaged in a regulative action which, unlike that of the vagus or sympathetic, is not a direct action on the heart itself, but is brought to bear indirectly on the heart through the instrumentality of the vascular (arterial) system. This nerve is the *depressor*. It is a branch of the vagus distributed to the heart—some say to the walls of the aorta—and from there runs up the neck as a separate branch in the horse, cat, and rabbit, but in other animals is contained in the trunk of the vagus. It joins the superior laryngeal nerve, and finally reaches a centre in the medulla which regulates the movements of the bloodvessels of the body, known as the *vasomotor centre*. The impulses which pass along it are afferent—viz., they pass to the central nervous system and not out of it. The heart in this way is placed directly in communication with the centre which presides over the vascular system, a centre by whose varying activities the arteries of the body are made smaller (constricted) or larger (dilated), according to the needs of the system. If the heart is labouring and its muscular structure becoming weakened, impulses pass up the depressor to the vasomotor centre, resulting in impulses being sent out which cause the abdominal arteries to dilate and hold more blood. By this means the peripheral resistance is diminished, the blood-pressure falls, and the heart is eased, since it now has less work to do in ejecting its contents.

If the depressor nerve be divided, no effect follows ; if the end in contact with the heart be stimulated, there is no result ; but if the central or upper end be stimulated, the blood-pressure falls (see Fig. 26).

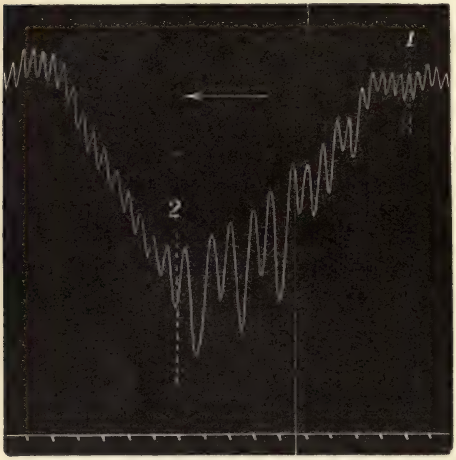


Fig. 26.—Blood-Pressure Tracing : Rabbit (Mercury Manometer) (Stewart).

Central end of depressor stimulated at 1 ; stimulation stopped at 2. Time trace, seconds.

By some the depressor nerve has been described as the sensory nerve of the heart, as there are signs of pain when it is stimulated in an animal not under an anæsthetic. But this view is not generally accepted, and as a matter of fact the heart may be handled, pinched, pricked, or otherwise injured, without provoking the least sign of pain on the part of the animal. Colin's experiments in this direction on horses appear quite conclusive. Not only is it considered that the external surface is insensible to pain, but the internal surface also ; for, as previously noted, the experimental introduction of foreign bodies into the cavities of the heart appears to produce no pain. Under pathological conditions the results are otherwise ; foreign bodies, so common in the heart of the cow, cause great suffering, therefore there must be sensory nerves, though normally their excitability is probably low.

It is supposed that in the heart or aorta the sensory nerve endings are stimulated by contraction, and that the impulses so obtained are conveyed to the medulla by the depressor, and maintain the tonic activity of the cardio-inhibitory centre. It can certainly be shown experimentally that every contraction of the heart sends a series of impulses up this nerve, but whether these are conveyed to the cardio-inhibitory centre has not been decided.

We have now seen how complex are the influences exercised by the nervous system in connection with the rhythm, force, and tone of the heart muscle, the moderating influence in these directions exercised by the vagus, and the stimulating functions of the sympathetic. The factors determining which influence at the moment is best suited to the existing conditions originate in the periphery, and not in the central nervous system ; from the periphery—viz., skin, muscles, viscera, bloodvessels, and heart—impulses are transmitted to the brain which are obeyed by the cardio-inhibitory or accelerator centres in the medulla.

The Chemical Stimulus.—One further feature in connection with the matter still remains for consideration, and that is the influence of certain 'internal secretions,' on increasing or diminishing the function of the heart muscle. It is now known that the adrenal capsules and pituitary body are capable of furnishing extracts which, when introduced into the circulation, exercise a powerful effect on the heart. An extract of the medulla of the adrenal capsules increases the rhythm, force, and tone of cardiac muscle ; an extract of pituitary body contains two substances : one increases the tone, but does not affect the rate of rhythm of the muscle, while the second substance diminishes the force of the heart-beat. It may well be that these ductless glands pour into the circulation their various secretions in the proportions suited to the most efficient working of the heart, and by their action on the nerve-centres maintain them in effective working order.* The action of these internal secretions on the movements of the bloodvessels will be referred to later.

Pathological.

Disease of the heart of the lower animals is uncommon. It might have been thought that horses would be particularly exposed to this class of trouble, bearing in mind the enormous strain placed on the heart during labour, and the utter want of consideration shown by the vast majority of those who ride and drive them. But it is not so. The hearts of horses exposed to the greatest strain seldom show any pathological change ; probably the most uncommon lesions found on post-mortem examination are those affecting the heart. The heart may dilate under strain, but such dilatation when accompanied by hypertrophy is compensated, and no indication of trouble exists during life. As evidence of the gross strain to which horses are exposed, ruptures of the heart are by no means uncommon. It is strange they are not more frequent. They probably would be but for the saving cause that degenerations of the heart substance are rare. When the heart ruptures, it gives way in the auricle, where the wall is thinnest—so thin, indeed, that in certain parts of the auricle daylight may easily be seen through the tissue. It is generally the right and not the left auricle which suffers, showing how great is the resistance offered by the pulmonary vessels as the result of engorgement due to severe work.

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* See 'The Factors which make for an Efficient Circulation,' by Professor E. A. Schäfer, F.R.S., *British Medical Journal*, October 29, 1910.

Valvular disease is not unknown, but so rare that probably there is no practitioner with a large experience in the examination of horses for soundness who ever thinks of examining the heart! On the other hand, irregularities in the heart's action are very common, frequently purely functional in character, unassociated with organic change, and do not interfere with the usefulness of the animal. A horse condemned for heart disease on the strength of an intermittent pulse may remain a living reproach to the practitioner.

The views regarding heart disease in man have within the last few years been undergoing profound modification at the hands of Mackenzie, Lewis, and other workers. It is too much to expect that the complete revolution in doctrine which these necessitate will be at once brought about; the process must be gradual, but when accomplished it will be found that very little modification from the views now put forward will be found necessary. Briefly, the modern view of the causes of heart failure looks to the heart muscle itself as the prime seat of disorder, while the coarser and more obvious conditions, such as murmurs and irregularities, may not even be pathological, or, if pathological, are of secondary interest to the all-important inefficiency existing in the heart muscle. Mackenzie has recently* presented a statement of the modern views of heart trouble in man, of which the following is a brief epitome:

The popular conception of heart failure is associated with valvular trouble, the thickened and shrunken valve producing incompetence, with leakage from the ventricle, distension of the auricle, stasis in the lungs, back pressure into the veins, with consequent dropsy. Functional murmurs may exist in a perfectly healthy heart under physiological dilatation; a tricuspid regurgitation may be regarded as a safety-valve function, as it is in certain diving animals; and a mitral regurgitation may exist for fifty years without crippling the heart in its work. Irregularities of the heart may not only be normal, but even, within certain limits, considered as evidence of the integrity of the heart muscle.

These unorthodox views from the mouth of one who has confined his attention to the study of heart trouble for many years, must cause even the most sceptical to pause. According to Mackenzie, the essential causes of heart trouble in man are due to auricular fibrillation, a condition which alters the whole aspect of the mechanism of heart failure. To the phenomenon of fibrillation attention has been drawn at p. 47. The muscle fibres, instead of contracting in a normal and orderly manner, contract irregularly, rapidly, and independently, so that the chambers not only cease to contract as a whole, but actually stand still, while all their fibres are in incessant movement. When this condition occurs in the ventricles, sudden death ensues ; when it occurs in the auricles, death does not follow, for fibrillation cannot pass along the bundle connecting the auricles with the ventricles. The degree of heart failure which follows auricular fibrillation depends upon the extent to which changes have occurred in the structure of the heart muscle of both auricle and ventricle.

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* 'Heart Failure,' James Mackenzie, M.D., LL.D., *British Medical Journal,* April 8, 1911, p. 793.

In severe inflammatory chest invasions of the horse, the heart, but especially its sac, may become acutely affected. There are few attacks of severe pleurisy in the horse which are not associated with pericarditis, followed not only by great thickening of the heart sac, but by more or less extensive effusion into it. The heart then becomes enveloped in a water jacket, which greatly adds to the gravity of the case. In the above acute cases the heart muscle suffers, and hæmorrhages into it are common and widespread.

In the dog the heart's action is normally intermittent.

Foreign bodies in the heart of cattle, especially cows, are well known, and give rise to a peculiar train of symptoms. Vegetations on the valves of both the dog and pig are recognised in connection with certain infectious diseases.

be seen, for instance, at post-mortem examinations. The veins as they pass from the capillaries towards the heart become reduced in number and increased in size, and they terminate in the right auricle of the heart by means of two trunks, the united areas of which greatly exceed that of the aorta.

In the veins valves are found. These are well marked in the veins of the head, neck, and extremities. The valves look towards the heart, and supply a simple and essential means of insuring the return flow of the blood along the veins to the heart. In certain places the veins have no valves, such as the large veins entering the heart, those of the bones, the abdominal veins, and the veins of the foot and brain.

Veins are normally pulseless, but under certain conditions a pulse-wave may pass through the capillaries into the veins, producing a *venous pulse*. The best physiological example of this form of pulse can be experimentally produced by stimulation of the *chorda tympani*, a nerve supplying the submaxillary gland with fibres which cause the bloodvessels to dilate. Under stimulation the vessels dilate, the veins pulsate, and even the blood coming from them is arterial in colour. Another form of venous pulse is met with in the great veins at the root of the neck; the mechanism of the pulsation in these has already been explained (see p. 38). It is abnormal for pulsations to extend any distance up the jugular vein; when this occurs the explanation is pathological, not physiological.

Mechanics of the Circulation.—At each systole of the ventricle a certain amount of blood is forced under great pressure into an already full aorta, and imprisoned there by the closure of the aortic valves. The aorta dilates to receive this extra blood, because, owing to the friction in the smaller vessels, or, as we shall speak of it, the *peripheral resistance*, it is impossible for the amount pumped into the aorta at each systole to pass out at once at the periphery; in this way high blood-pressure is produced in the arteries. The increase in the size of the aorta to accommodate this extra blood commences near the heart, and runs as a wave to the periphery; this wave is the *pulse*.

The two important points in the circulation which we have now to consider are blood-pressure and pulse, and to understand these it is necessary that we should study briefly the laws which govern the flow of fluids through tubes.*

If water be pumped through a rigid tube or pipe, at every stroke of the pump as much fluid passes out at the further end of the tube as enters it at the other. Between the strokes of the pump no fluid issues from the pipe ; the jet is only produced at the moment the pump is in action. No more water can enter this rigid tube from the pump end than can leave it at the outlet. If now water be pumped through a *short* elastic tube, the outlet of which is in no way obstructed, the current of water through it behaves just as if it were a rigid tube—viz., a stream of water issues from the outlet during the action of the pump, and nothing more happens until the next stroke. An important alteration can, however, be made to the current through the elastic tube, by offering an obstruction at the outlet to the free passage of the water. The effect of this obstruction is that the elastic tube expands to accommodate the contents, while a stream pours from the partly obstructed outlet which no longer corresponds to the stroke of the pump, but is a continuous stream which issues so long as the pumping is continued. This continuous stream is produced by the elastic recoil of the tube keeping up the pressure which the pump imparted to the fluid, and the reason why the elastic recoil of the tube is now brought into play is owing to the partly obstructed outlet, or, as we have already termed it, the *peripheral resistance.* If the elastic tube be of sufficient length, a continuous stream will issue in spite of the absence of an obstruction ; this is brought about by the internal fluid friction against the walls of the tube, which of course causes a peripheral resistance. In elastic tubes, therefore, the recoil of the tube converts an intermittent into a continuous flow, and the distension of the tube which produces the recoil is caused by the *peripheral resistance.*

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* The subject of the movement of fluids in tubes is not only an extremely difficult branch of physics, but one still imperfectly understood. We have introduced less of it into this chapter than appears in most works on physiology, and, in fact, have only touched on those general principles which have a direct bearing on the circulation.

Whether in a living tube like a bloodvessel, or in a dead tube like a pipe, fluid flowing under a head of pressure meets with resistance ; this is due to friction of the fluid particles against the wall of the tube. The amount of resistance is not the same throughout the length of the pipe : it steadily decreases to the exit ; but this assumes that the pipe maintains an even bore throughout. If the pipe were to narrow at any point in its length, the friction would in consequence increase at that particular place. The resistance or pressure due to friction may be estimated at any part of the tube by the introduction of a gauge—viz., a vertical tube placed at right angles to the flow. In this tube the fluid will rise to a certain height, and the weight of the fluid column indicates the pressure exerted at that particular spot. Such a tube is known as a *manometer,* and the pressure it gauges is the *side* or *lateral pressure* due to frictional resistance.

Of the total force or head of pressure engaged in forcing fluid along a tube, the bulk is used up in overcoming the frictional be seen, for instance, at post-mortem examinations. The veins as they pass from the capillaries towards the heart become reduced in number and increased in size, and they terminate in the right auricle of the heart by means of two trunks, the united areas of which greatly exceed that of the aorta.

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Of the total force or head of pressure engaged in forcing fluid along a tube, the bulk is used up in overcoming the frictional resistance, the balance imparts to the fluid a certain velocity, and the remaining pressure is known as the *pressure velocity*.

The whole mechanics of the circulation can be worked out on a model consisting of a syringe to represent the heart, elastic tubes to represent the bloodvessels, and a few clamps to offer the needful peripheral resistance. With such a model, if water be forced into the arterial tubes, the clamps being open and the peripheral resistance therefore very small, it is found, by means of a manometer, that the pressure in the arterial tube rises with each stroke of the syringe, and falls with the free pouring of the contents into the tubes representing the veins. As the peripheral resistance is small, the pulsation set up in the fluid readily passes into the veins, and a manometer will here register nearly the same rise and fall as was met with in the arteries.

If, however, the vessels be clamped so as to produce a resistance, the first stroke of the pump causes the arteries to become distended; they then recoil, and while undergoing this they receive another stroke from the pump and become still more distended. Once more they recoil on their contents, and are once more distended by the action of the pump, and so on. If during this time the arterial manometer be watched, it will be observed that the mercury or water rises with each stroke of the pump, but instead of falling at once to zero as it did in the unclamped tube, it only has time to fall a short distance before a second stroke of the pump sends it still higher than before; this is repeated at every stroke of the pump until the water or mercury refuses to rise any higher in the tube, contenting itself by rising to a certain height at each stroke of the pump, and falling to a certain level during the interval between one stroke and another. In other words, a mean pressure has been established in the tubes representing the arteries, which has been brought about by the *peripheral resistance*, the elastic recoil of the tube, and the pumping of the syringe. So long as these factors remain the same the mean pressure will not vary. If, however, the clamped vessels be released, so as to allow fluid to flow more easily into the tubes representing the veins, the manometer at once shows a fall in the mean pressure owing to the removal of a certain amount of resistance, and by removing this resistance completely the mean pressure falls to zero. The *mean pressure*, then, represents the force which is necessary to cause as much fluid to pass through the periphery as is being pumped into the system of tubes by the syringe; if the peripheral resistance is high the pressure is high, and *vice versa*.

A careful study of this experiment places us in complete possession of the main facts of the circulation, but even up to this point we have not learnt all the lessons it is capable of teaching.

If a manometer be placed on the venous side of the model, it will show a very low pressure at the time when the arterial pressure is high. If the arterial tubes be felt it will be observed that at each stroke of the pump they expand, producing what is known in living tubes as the *pulse;* this expansion of the tube is greatest nearest to the syringe, dying out entirely at the peripheral resistance. It is evident that if we loosen the clamps, and so reduce the resistance and lower the mean pressure, that pulsatile waves will pass over to the venous side of the model, and these can again be obliterated by screwing up the clamp. Lastly, our model, if working at mean pressure, will show the effect of injury to the arterial tubes ; if these be pricked, a continuous jet of water shoots out, the strength of the jet varying with each stroke of the syringe, whilst an injury to the venous side produces no jet of water, but only a trickling flow.

Practically this embraces our knowledge of the main facts of the circulation, for all we have found true of syringe, elastic tubes, and clamps, will be found true of heart, bloodvessels, and peripheral resistance. The heart has to keep the arteries full ; the innumerable smaller arteries with their muscular coat supply the peripheral resistance. Under the influence of this and the contraction of the left ventricle, the pressure in the arteries rises so high, and their distension is so great, that as much blood passes through the periphery during the contraction of the heart and the ensuing pause as enters the aorta during the contraction of the left ventricle. The elastic system of arteries insures that an intermittent is converted into a continuous flow, and thus a perpetual pressure is kept up on the mass of blood during the heart's pause. By a contraction of the arterioles the peripheral resistance is increased and the blood-pressure raised ; by a relaxation of the arterioles the peripheral resistance is reduced and the blood-pressure falls. We have stated that a contraction of the arterioles by increasing the resistance raises arterial pressure and as a rule lowers that in the veins. This holds equally true for the pressure conditions in the vessels of any locally circumscribed area of the body as for the vascular system generally. It must not, however, be forgotten that local effects may and do produce general effects. If, for instance, *one* artery alone contracts, this must lead to an increase of arterial pressure, which produces an increased flow of blood through all the simultaneously uncontracted arteries on into the veins. When the contracted artery is small, so that the area it supplies is limited, the local effects are more marked than the general effects. If, on the other hand, the local area affected is at all large, the influence of changes in the arteries of this area on the general blood-pressure may be very obvious. We shall meet with a striking instance of this when dealing with the action of the depressor nerve on blood-pressure, through the medium of alterations in the arteries which supply the splanchnic area, brought about by means of the splanchnic nerve.

Blood-Pressure.—From what has been said, it is hardly necessary to define blood-pressure as the pressure exercised upon the blood in the elastic vessels, resulting from the action of the heart and the peripheral resistance.

If the peripheral resistance is great through a contraction of the arterioles, the amount of fluid passing into the veins is reduced in quantity ; a larger bulk of fluid will in consequence exist between the pump and its outlets, and the blood-pressure rises. If, on the other hand, the blood is passing freely through the dilated arterioles, the blood-pressure falls. When the heart is more active, or when the arterioles contract, the blood-pressure rises ; when the heart is less active or the arterioles dilated the blood-pressure falls.

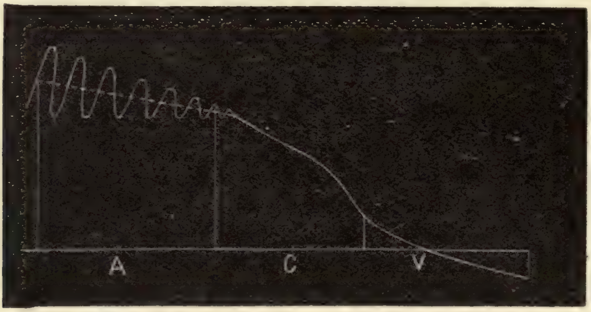

FIG. 27.—DIAGRAM TO ILLUSTRATE THE SLOPE OF PRESSURE ALONG THE VASCULAR SYSTEM (STEWART).

A, Arterial ; C, capillary ; V, venous tract. The interrupted line represents the line of mean pressure in the arteries, the wavy line indicating that the pressure varies with each heart-beat. The line passes below the abscissa axis (line of zero in atmospheric pressure) in the veins, indicating that at the end of the venous system the pressure becomes negative.

The mean pressure in the arteries is highest close to the aorta and lowest in the region of the periphery ; the fall in pressure from the aorta to the periphery is gradual. At the minute arterioles the fall in pressure is rapid, and in the veins gradual and very slow ; in fact, owing to causes to be dealt with in the chapter on Respiration, a negative pressure may exist in the great veins near the heart. Fig. 27 exhibits in a graphic form the fall in blood-pressure in the different regions of the vascular system.

It has been seen that the amount of side pressure exercised by fluid in a tube is ascertained by means of a manometer; precisely the same principle is employed to ascertain the side pressure in a bloodvessel, here called blood-pressure. It is interesting to observe that the first blood-pressure experiment ever performed was carried out on a horse, a vertical tube being placed in the femoral artery, in which the blood rose to a height of 8 feet 3 inches. It is, of course, for several reasons inconvenient to work with a long tube, and in consequence most manometers are **U**-shaped tubes containing mercury which is made to balance the pressure to be measured. The greater specific gravity of this metal enables a tube nearly fourteen times shorter to be employed. The inertia of mercury renders it useless for recording delicate or sudden alterations in pressure; these are obtained by means of spring manometers.

In Fig. 28 is shown the apparatus employed in determining blood-pressure with the ordinary mercury manometer.

The *Mean Arterial Pressure* is increased at each systole of the ventricles, and falls at each diastole; the maximum pressure is therefore known as systolic, the minimum as diastolic. In the aorta of the dog the systolic pressure may be 168 mm. (6¾ inches), the diastolic only 100 mm. (4 inches). The difference between these two pressures is sometimes spoken of as the *pulse pressure* or *mean pressure*. The further the vessel is situated from the heart, the less the difference between systolic and diastolic pressures, until finally in the capillaries there is no difference, and consequently no pulse.

In the aorta of the horse the blood-pressure may vary from 321 mm. to 150 mm. (12½ inches to 6 inches); dog, 168 mm. to 100 mm. (6¾ inches to 4½ inches); sheep, 206 mm. to 156 mm. (8 inches to 6¼ inches).

In the carotid of the horse the pressure is from 325 to 215 mm. (12¾ inches to 8 inches), equal to a column of blood 9¼ feet to 13¾ feet in height.

Neither size of body nor pulse-rate bear any relation to the amount of blood-pressure present in the arteries of an animal. The pressure in the carotid of the goose is nearly the same as in the carotid of the horse.

Influence of Muscular Work on blood-pressure is very marked; the pressure is raised because muscular contraction causes mechanical compression of the vessels of the muscles. Every movement of the body, every movement of a limb or part, affects the blood-pressure in it; in the large arteries the pressure from this cause will be found to be constantly varying, unless the animal be absolutely immobilised. There is also another important cause—viz., the increased force and frequency of the heart-beat.

Effect of Gravity on Blood-Pressure.—L. Hill has demonstrated the influence on the blood-pressure of hydrostatic pressure due to gravity. He has shown in man that the arterial pressure is higher in the erect than in the horizontal position ; that it is higher in the leg than in the arm to the extent of the column of blood separating the two points of measurement. Whether the body is placed in the horizontal, vertical, or inverted position, the blood-pressure in those arteries at the same level as the heart remains little altered, but in the vessels below the heart the pressure is increased. Constant compensations are occurring in the circulatory system to guard against important alterations in blood-pressure due to gravity. These are effected by a variable output of blood from the heart, but especially by dila-

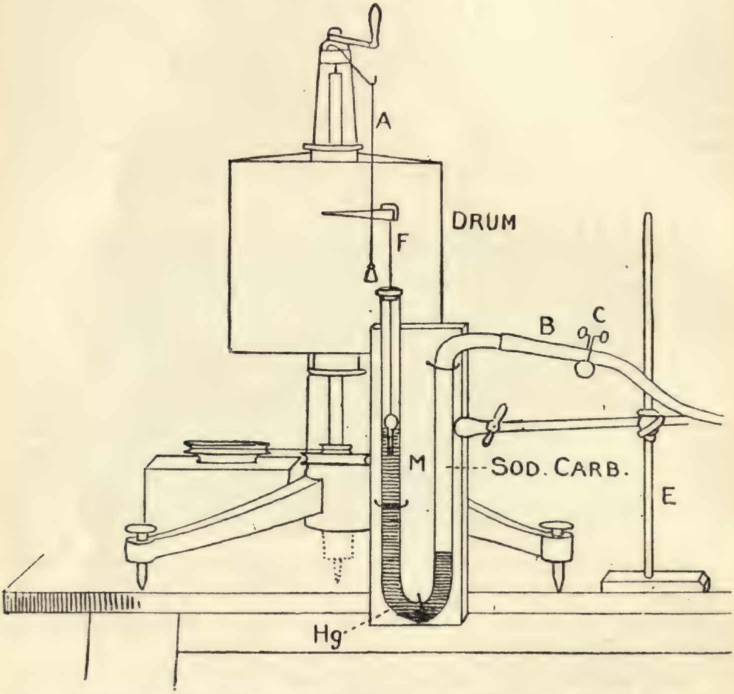

FIG. 28.—ARRANGEMENTS FOR TAKING A BLOOD-PRESSURE TRACING (STEWART).

M, Manometer ; Hg, mercury ; F, float armed with writing-point ; A, thread attached to a wire projecting from the drum, and supporting a small weight. The thread keeps the writing-point in contact with the smoked paper and the drum. B is a strong rubber tube connecting the manometer with the artery ; C a pinch-cock on the rubber tube, which is taken off when a tracing is to be obtained.

tation or constriction of the splanchnic area. Under abnormal conditions, such as ill-health, these compensations are absent or imperfect, and anyone who has been in bed for a few days, and then assumes the vertical position, knows the faintness which follows from the general fall in blood-pressure due to dilatation of the splanchnic area. If the ordinary hutch rabbit be held in the vertical position for a period varying from one-quarter to three-quarters of an hour, it will in all probability die. The cause of death is cerebral anæmia; under the influence of gravity the blood collects in the splanchnic area and the blood-pressure in the aorta falls. With a wild rabbit, dog, or cat, this experiment fails, the explanation being that the tense abdominal walls of the animal leading an active life compresses the splanchnic area and prevents the blood collecting in the abdominal cavity. In a dog or cat previously poisoned by chloroform or chloral the experiment succeeds, as the tone of the abdominal walls is lost. When a horse rears up and falls backwards, it may be due to temporary cerebral anæmia resulting from want of compensation in a vertical position, apart from any question of loss of balance.

The arterial pressure varies, as has been said, with each systole of the ventricle, but besides this there are also certain larger and longer undulations obtainable in graphic records of blood-pressure which hitherto have not been regarded by physiologists as connected with the heart, but caused by the movements of respiration. It has been observed that inspiration causes a rise and expiration a fall in pressure. This important action of the respiratory pump has never been quite satisfactorily explained, and we now have the view of T. Lewis, who finds that the rise of pressure on inspiration is due to the lessened pressure in the pericardium and consequent increased filling of the heart. If the pericardial sac be opened to the air, no such curves are produced. Lewis therefore concludes that the effect produced is due entirely to the heart, brought about by changes in the intrapleural pressure. The question will be again examined in dealing with respiration. The character of the curve produced is seen in Fig. 29.

The *Blood-Pressure in the Capillaries* is very difficult to ascertain. It is probably $\frac{1}{9}$ to $\frac{1}{7}$ of that in the large arteries or lies between 20 to 40 mm. of mercury.

Hill compares the capillary system to a sponge, squeezed and filled continuously by the active motions of the body. The contents of the capillary vessels are constantly being pressed onwards by muscular movements, so that the pressure in them must be continually varying. Hill has shown in the human subject that in an arm held down, the fist being clenched, the pressure in the arteries and veins is high, but in the capillaries of the fist it is *nil*, owing to their compression.

Blood-Pressure in the Veins is $\frac{1}{14}$ or $\frac{1}{15}$ of that in the large arteries. The greater the distance the veins are from the heart, the greater the pressure, so that the highest pressure is in the peripheral veins and the lowest in the jugular. In a sheep the following values were obtained :

Jugular vein	0·2 mm.	($\frac{1}{100}$ inch).
Facial vein	3 ,,	($\frac{1}{8}$ inch).
Brachial vein	12 ,,	($\frac{7}{16}$ inch).
Crural vein	14 ,,	($\frac{1}{2}$ inch).

The venous pressure in a dependent part such as the limbs is higher than in a part like the head and neck, where the venous flow is assisted by gravity. During work the venous pressure in the limbs rises, due to the increased ventricular output, constriction of the abdominal veins, and compression of the veins of the limbs. A distended condition of the heart also causes the venous pressure to rise, owing to diminished intake.

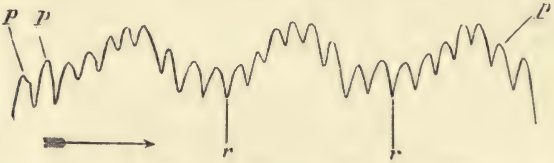

Fig. 29.—Tracing of Arterial Pressure with a Mercury Manometer (Foster).

The smaller curves *P, P* are the pulse-curves due to the heart-beat. The space from *r* to *r* embraces a so-called respiratory undulation. The tracing is taken from a dog, and the irregularities visible in it are those frequently met with in this animal.

In the large veins just as they enter the heart the pressure is very low. The manometer may even at intervals show a negative pressure. In the anterior vena cava of the dog a negative pressure of -3 mm. ($\frac{1}{8}$ inch) may be registered. The negative pressure in the veins entering the thorax is due to the fact that the pressure within that cavity is below that of the atmosphere, so that an aspirating effect is produced upon the blood in these veins. It is this aspirating action which renders operations at the root of the neck in the human subject dangerous should air enter the wounded veins. Judging from the writer's observations on the horse, blowing air into the veins causes no discomfort until a considerable amount has been introduced ; even then only sighing respirations are produced.

Blood-Pressure in the Pulmonary System.—The variations in pressure in the pulmonary system are very much less than those occurring in the general circulation, and are believed not to exceed 15 to 20 mm. (¾ inch) of Hg.

In the pulmonary artery the pressure is only about one-seventh of that in the aorta. This pressure decreases throughout the entire pulmonary channel up to the left auricle. The resistance offered by the pulmonary capillaries is less than the peripheral resistance experienced in the systemic circulation.

Influence of Hæmorrhage on Blood-Pressure.—The amount of blood which may be removed from the body without lowering the blood-pressure is surprising. This is explained by the fact that the vessels adjust themselves to the reduced bulk of fluid in circulation ; this adjustment is effected by means of a nervous apparatus to be dealt with presently, and in this way the blood-pressure is kept up. Experiments show that it is not until two-fifths of the blood in the body have been removed that the blood-pressure begins to fall; after cessation of hæmorrhage the pressure again rises, unless the loss of blood amounts to 3 per cent. of the body weight, in which case the low pressure becomes dangerously permanent.

Stewart's observations on dogs show that an animal may recover even after losing more than half its blood.

We have previously referred to the question of blood-letting ; the boldness with which our forefathers used the lancet, especially those who believed in a heavy bleeding to begin with, is justified by the physiological evidence above mentioned—viz., that it is not until about one-quarter of the blood in the body is drawn off that any effect on the blood-pressure is evident.

It is astonishing how rapidly a deficiency in the circulating fluid is made good, the fact being that the tissues give up their fluid in an endeavour to replace the loss of blood, quite apart from the repair which is being effected through the thoracic duct. It is the loss of fluid by the tissues which causes the thirst of hæmorrhage.

Hill has shown that the effect on the blood-pressure of increasing the volume of fluid in circulation is very slight. The arterial pressure and that in the venæ cavæ rises with the injection, but soon falls to its old level, the injected fluid being disposed of in the dilated venous reservoirs, especially those of the splanchnic area. Animals which have been transfused to the extent of 10 or 12 per cent. of the body weight—viz., more than twice the normal amount of blood—suffer from heart failure, the blood-pressure rising and falling as the overloaded heart does its best to cope with the difficulty. Excessive transfusion can best be borne if carried on slowly, in order that the large abdominal veins and those of the liver may be given time to accommodate the increasing bulk of fluid.

The influence of the nervous system on blood-pressure will be studied presently.

Circulation in the Living Tissues.—The circulation in the living animal may be readily seen in the web of a frog's foot, or in the mesentery of a mammal, and in this way we learn exactly how the corpuscles behave within the vessels.

In all capillary vessels of small size the corpuscles pass through singly, sometimes revolving in the plasma, traversing certain sections very rapidly, others very slowly. In the vessels larger than the capillaries, such as the commencement of the small veins, the stream of blood behaves somewhat differently ; in these the centre of the vessel is occupied by a rapidly moving column of red cells, the *axial* stream, whilst between them and the coats of the vessel is a clear layer or zone, the *inert* layer, in which may be seen the white corpuscles strolling lazily along the sides, occasionally stopping, then moving forward once more. This difference in the behaviour of the corpuscles is due to the physical fact that the friction against the sides of the vessel is greater than in the centre, and the red corpuscles being heavier than the plasma, are drawn into the rapid part of the current. This also explains why the lighter leucocytes hug the wall of the vessel, through which, as previously pointed out, they may pass in order to gain the tissues without.

Under the influence of inflammation the slowly moving leucocytes attach themselves to the wall of the capillaries and venules, and pass into the tissues in large numbers. Small numbers of red corpuscles may also pass out. This process is known as *diapedesis.* Inflammatory changes are essentially due to the cell wall, and not the blood, and this is proved by the fact that an artificial corpuscular fluid introduced into an inflamed area behaves exactly as does the blood.

The Pulse.—When the left ventricle contracts it drives a new supply of blood into an already full aorta, and room for it has to be found. This can be effected in one of two ways, either by displacing an equal volume of fluid already in the system, or by temporarily making the artery larger. The latter process is followed as being the most economical in energy. The aorta distends to receive the additional blood, followed by an elastic recoil of its walls which drives more blood along another segment of the vessel ; this accordingly distends and then recoils, and so the process is repeated as a wave throughout the arterial system. This distension and elastic recoil is the pulse.

Each expansion of the arterial wall coincides with a contraction of the ventricle, and so each beat or throb of the pulse corresponds to a contraction of the heart. The rhythmical force of the heart is stored up in the arteries as elastic recoil ; this intermittent expansion and contraction of the arteries gradually becomes less marked at a distance from the aorta, and dies out at the arterioles.

Attention has previously (p. 65) been drawn to the fact that the *elastic* properties of the arterial wall, together with the *peripheral resistance* in the smallest bloodvessels, convert the intermittent flow started by the heart into the continuous stream in the capillaries and veins. In seeking for the cause of the disappearance of the pulse, we find it similarly in the elastic property of the arterial walls. In virtue of this property each inch of the arteries is engaged, by means of its sudden distension after each heart-beat and its more gradual elastic recoil before the next, in sheltering the capillaries from the effect of that beat. The oscillations of pressure which give rise to the pulse are, so to say, ' damped ' by the elastic arterial walls, or in other words converted into a steady pressure, a fraction of the pulse being thus actually destroyed by each inch of the arteries. When all the fractions thus destroyed are added together, we can readily understand why the initial ' jerk,' to which the pulse is due, has entirely disappeared just before it would otherwise have reached the capillaries. If the arterioles dilate considerably, when, in fact, less elastic recoil of their walls is called into play by the lessened peripheral resistance, it may be possible for the ' throb ' to pass not only through the arterioles but also the capillaries, and appear in the veins ; in this way a venous pulse may be produced. An example of this has been given on p. 67.

The intermittent expansion of the arteries, called the pulse, travels from the aorta to the periphery, and produces a wave in the arterial system which is spoken of as the *pulse-wave.* From what has been said it is evident that the height of this wave is greatest nearest the heart, and falls to zero at the capillaries. The wave travels with considerable velocity, from 4½ to 9 metres (15 to 30 feet) per second. This may easily be determined by noting the interval between the commencing successive rises of two levers, resting consecutively on the wall of an artery, at a measured distance apart. The length of the pulse-wave is also considerable—viz., about 5½ metres (18 feet). This is arrived at by noting the time each single pulsation, travelling with the previously determined velocity, takes to pass completely under any *one* lever. Putting these data together, it is evident that the beginning of each pulse-wave is lost in the arterioles before its end has left the aorta.

No mental confusion should exist as to the difference, and the causes of that difference, between the velocity of the pulse-wave and the velocity of the onward flow of the blood. The factors which give rise to them are quite distinct. The pulse-wave runs along the surface of the blood-stream ; the blood-current runs, as it were, within the pulse-wave ; the former travels at a high speed, the latter comparatively slowly, at most some 381 mm. (15 inches) per second. The case is similar to that of a wave seen moving rapidly over the surface of a slowly flowing stream.

The pulse-wave can be studied by means of the graphic method ; it is obvious that a lever placed on a pulsating vessel will be moved up and down, and may be made to trace a curve which will record the passage of the pulse-wave under the lever at that particular spot. A tracing thus obtained, known as a *sphygmogram,* simply registers the expansion and recoil of the artery while the wave is passing ; it will not give a tracing of the pulse-wave itself, which, as we have seen, is 18 feet in length, but it gives the details of the *form* of the wave. But it may be at once said that unless the proper degree of pressure is kept on the vessel, great irregularity in the sphygmograms will be produced, due to instrumental errors, and not to the true pulse-wave.

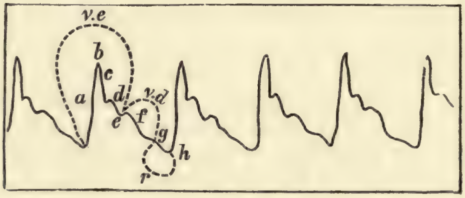

Fig. 30.—Normal Sphygmogram modified from Dudgeon ; Pressure 2 Ounces (Hamilton).

v.e, The period of ventricular systole ; *v.d,* the period of ventricular diastole ; *r,* the period of rest ; *a, b, c,* primary or percussion wave ; *d,* first tidal or predicrotic wave ; *e,* aortic notch ; *f,* dicrotic wave ; *g,* second tidal wave.

The simplest description of a sphygmogram (Fig. 30) is that it consists of a nearly vertical unbroken upstroke (the *anacrotic* limb), and an oblique downstroke (the *catacrotic* limb), which is broken by two or three waves known as *catacrotic waves.* Of these two or three waves *f* (Fig. 30) is one of the few which occurs with any regularity, and is known as the *dicrotic* wave. The notch *e* is described as the aortic notch, and is caused by the closure of the aortic valves. The dicrotic wave is produced by a recoil of blood, the result of closure of the aortic valves ; this reflected wave passes from the centre over the whole arterial system. The smaller waves in the catacrotic limb are either vibrations of the arterial wall, or reflections of the pulse-wave from the periphery towards the heart. That the dicrotic wave is a reflection from the aortic valves, is shown by the tracing in Fig. 31, taken from the facial artery of the horse, *A* before, and *B* after destruction of the valves. In *B* the dicrotic wave has disappeared. A well-marked dicrotic pulse gives a double beat of the pulse for each single contraction of the heart (see Figs. 32 and 33). Venous pulse tracings are referred to at p. 44.

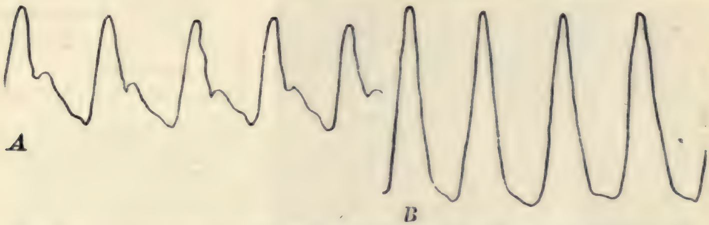

FIG. 31.—TRACING FROM THE FACIAL ARTERY OF THE HORSE (HAMILTON).
A, before, *B* after destruction of the aortic valves.

The pulse-wave distends all the arteries of a part, and by so doing actually increases the volume of the organ at the moment of its passage; this has been described as the **volume pulse**, and it can be recorded in the following manner: A limb, a kidney, or spleen, is placed in a closed chamber containing fluid; at each passage of the pulse-wave the volume of the part, being increased, causes an increased pressure in the fluid, and this, by means of any of the methods of registering changes of pressure in a fluid, may be made to furnish a graphic record. Such an instrument is known as a *plethysmograph*, and in Fig. 34 the apparatus may be seen as applied to the arm. So sensitive may this method of registration be made, that a tracing of

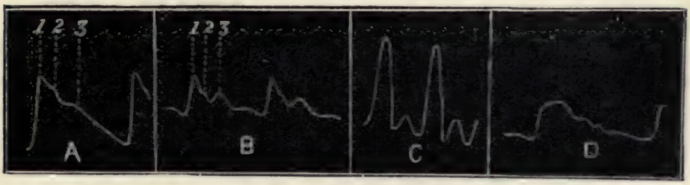

FIG. 32.—PULSE TRACINGS (STEWART).

1, Primary elevation; 2, predicrotic or first tidal wave; 3, dicrotic wave. The depression between 2 and 3 is the dicrotic or aortic notch; 3 is better marked in B than in A. C, dicrotic pulse, with low arterial tension; D, pulse with high arterial pressure, summit of primary elevation in the form of an ascending plateau.

volume pulse may show not only every beat of the heart, but even the dicrotic wave (see Fig. 35).

In connection with pulses the term **tension** has been employed by pathologists ; thus pulses of high and of low tension have been described, and an attempt has been made to distinguish between the pathologist's tension and the physiologist's pressure. If tension be defined as the elastic force exerted by the artery on the blood within, it is evident that this bears some distinct relation to the force distending the artery—viz., the blood-pressure ; a high blood-pressure and high arterial tension describe the same conditions. In an artery giving a high tension the dicrotic wave is nearly extinguished, the vessels in fact are so full that the recoil wave makes very little impression on the tense arterial wall ; when blood-pressure is low and the amount of movement in the artery great, the recoil or dicrotic wave is very marked (Figs. 32 and 33).

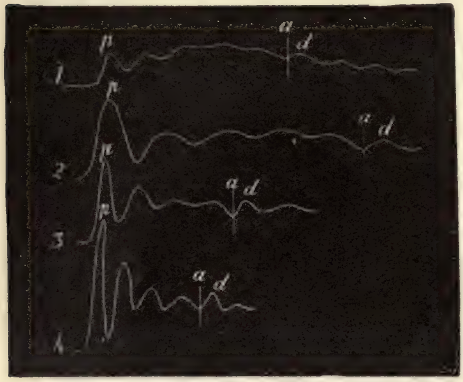

Fig. 33.—Curves of Blood-Pressure taken with a Spring Manometer from the Carotid Artery of a Dog (after Hürthle).

When 1 was taken the blood-pressure was high ; 2 corresponds to a medium ; 3 to a low ; and 4 to a very low pressure ; *p* is the primary elevation. This and the succeeding elevations between *p* and *a* are called 'systolic waves.' The systolic waves are followed by a marked elevation, *d*, which corresponds to the dicrotic wave.

The pulse varies in character, depending upon age, condition, and state of the system ; it also differs according to the class of animal. The following table shows the pulse-rate in different animals :

Elephant	25 to	28	beats per	minute.
Camel	28 ,,	32	,,	,,
Horse	36 ,,	40	,,	,,
Ox	45 ,,	50	,,	,,
Sheep	70 ,,	80	,,	,,
Pig	70 ,,	80	,,	,,
Dog	90 ,,	100	,,	,,

Certain variations occur in the pulse-rate. It is always much quicker in the young animal than in the adult. The heart of a foal at birth beats 100 to 120 per minute, and that of a calf 90 to 130 per minute. As the animal increases in age the pulse-rate drops, and in old age the pulsations are not only reduced in number but weaker.

The rigid condition of the arterial wall alters the shape and nature of the pulse tracing in old age.

Between size of body and pulse-rate there is a distinct connection; it varies inversely as the height—in the elephant 27 beats a minute, in the mouse 670.

The heart-rate is rapidly responsive to all outside influence, such as excitement or fear. A harsh word, fear, or timidity will cause the pulse of a nervous animal to register nearly double the number of beats of the heart. To sickness or injury the pulse is instantly responsive, and is one of the cardinal aids both in diagnosis and prognosis. Variations of pulse-rate follow as the result of work, so that a marked increase in the number of beats occurs; this means a larger amount of blood in circulation through tissues in a state of activity, and which consequently are in urgent need both of repair and flushing.

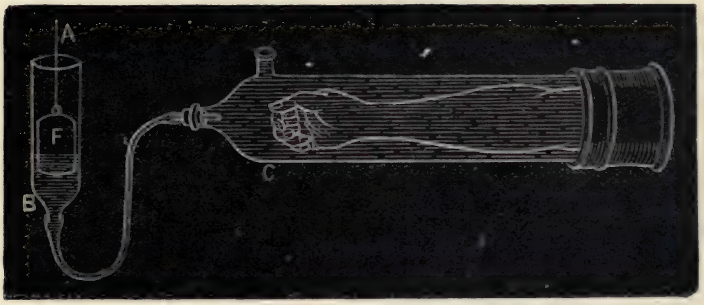

Fig. 34.—Plethysmograph for Arm.

F, Float attached by A to lever, which records variations of level of the water in B, and therefore variations in the volume of the arm in the glass vessel C. Or the plethysmograph may be connected to a recording tambour. The tubulure at the upper part of C is closed when the tracing is being taken.

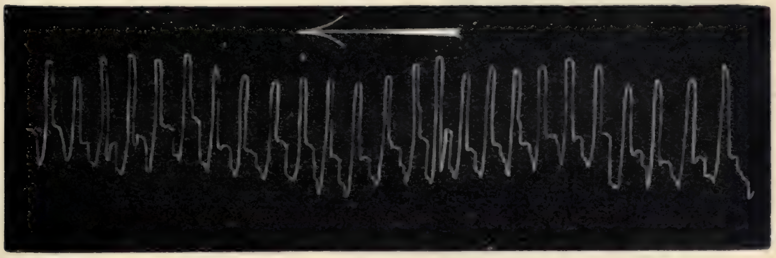

Fig. 35.—Plethysmograph Tracing from Arm (Stewart).

The tracing was taken by means of a tambour connected with the plethysmograph.

A relationship exists between the heart-rate and the condition of blood-pressure ; when the blood-pressure becomes low, the heart-rate increases as the result of reflex stimulation, by which means the output of blood is increased. If the temperature of the blood be raised, the heart-beat increases in frequency, and there appears but little doubt that one cause of the increased pulse-rate in fevers is the actual temperature of the circulating blood. If the temperature of the blood be raised experimentally, it is found that a point is reached at which the heart ceases to beat ; in the cat this has been found to be between 44° to 45° C. (111° to 113° F.).

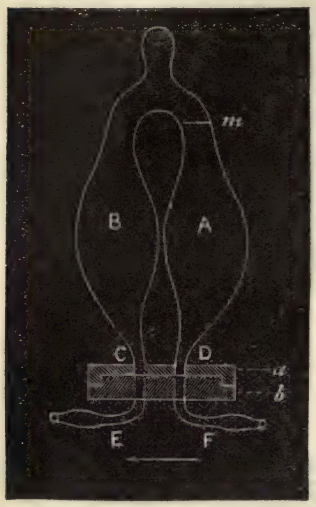

Fig. 36.—Stromuhr of Ludwig and Dogiel

A, B, Glass bulbs ; *a*, a metal disc, to which C and D are attached, and which can be rotated on the disc *b* ; E and F, cannulæ attached to *b*, and connected with the peripheral and central ends of a divided bloodvessel.

The **Velocity of the Blood** varies in the arteries, capillaries, and veins, being greatest in the former, least in the capillaries, and rising again in the veins.

The velocity of flow is inversely as the sectional area of the tubes ; the total sectional area of the capillaries is greater than that of the aorta, therefore the velocity is reduced ; from the capillaries to the heart the area becomes smaller and the velocity increases. The velocity of blood-flow depends on the width of the bed formed by the vessels ; as the arterial system expands the velocity diminishes ; in passing through the capillaries with their immense network the velocity is at a minimum ; in passing towards the heart the vessels are reduced in number, hence the bed is smaller, and the velocity accordingly increased. The cause of the flow throughout the entire system is the contraction of the left ventricle, and the gradual fall in pressure which occurs from the aorta to the right auricle.

The vascular system has been compared to two cones placed base to base, the apex of one being the left ventricle, of the other the right auricle ; where the bases of the two cones meet is the capillary network. The sectional area of this has been estimated by Volkmann as 800 times greater than that of the aorta, while owing to the width of the bed the passage of blood through it is 800 times slower than in the aorta.

Several ingenious instruments have been devised for the purpose of measuring the velocity of the blood. One, introduced by Ludwig, known as the *stromuhr* (Fig. 36), consists of a bulb of known size, and the length of time taken to fill this bulb of known capacity gives the velocity. The *dromograph* of Chauveau (Fig. 37) is employed for a similar purpose: it consists of a tube placed in the course of the vessel; within the tube is a plate; the blood streaming past this plate deflects a needle, and the angle of deflection may be expressed in terms of velocity.

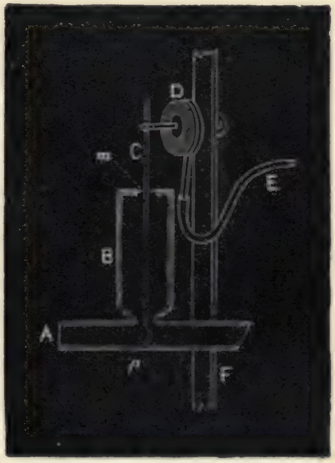

FIG. 37.—CHAUVEAU'S DROMOGRAPH.

A, Tube connected with blood-vessel; B, metal cylinder in communication with A. The upper end of B has a hole in the centre, which is covered by a membrane, *m*, through which a lever, C, passes. C has a small disc, *p*, at its end, which projects into the lumen of A, and is deflected in the direction of the blood-stream through A. The deflection is registered by a recording tambour connected with the lever C.

By means of these appliances the following velocities have been obtained in the vessels of the horse:

Carotid artery: 30 to 40 cm. per second (11·8 to 15·75 inches).
Metatarsal artery: 5·5 cm. per second (2·2 inches).
Jugular vein: 22 cm. per second (8·85 inches).

The velocity in the larger vessels is not constant; it is greatest during systole and less during diastole. Chauveau obtained the following results in the carotid of the horse:

During systole: 52 cm. per second (20·47 inches).
Beginning of diastole: 21·75 cm. per second (8·66 inches).
During the pause: 15 cm. per second (5·90 inches).

The mean velocity in the carotid of the dog is 26·5 mm. per second (10½ inches).

At the end of systole: 30·5 cm. per second (12 inches).
At the end of diastole: 21·5 cm. per second (8½ inches).

The difference between systolic and diastolic velocities becomes less and less as the small arteries are approached, until finally it disappears. We may say, therefore, that the velocity is more uniform in the small than in the large arteries.

The velocity of the blood is not as great as at first sight appears. If the stream in the carotid of the horse were never to diminish in velocity, it would cover less than 1¼ miles in an hour.

The velocity of the blood in the arteries furthest from the heart is less than in those nearest the heart ; for example, in the above table a horse with a carotid velocity of 30 to 40 cm. per second had a metatarsal velocity of only 5·5 cm. per second.

In the capillaries the velocity is very low, perhaps not more than 0·5 to 1 mm. ($\frac{1}{32}$ to $\frac{1}{16}$ inch) per second. This reduction, as we have seen, is due to the width of the bed through which the fluid is flowing. As the veins are reached and the bed narrows, the velocity increases, until finally, as the heart is approached, the velocity in the veins, though increasing, is much less than that in the corresponding arteries. A horse with a carotid velocity of 30·5 cm. (12 inches) gave a jugular velocity of 22·75 cm. (9 inches). It is generally considered that the velocity of the blood in the large veins entering the heart is about half as great as that in the aorta.

During work the velocity in the vessels increases. The flow of blood through the carotid of the horse has been observed by Lortet to be five or six times greater during the time the animal is feeding than when at rest.

In speaking of blood-pressure we drew attention to the fact that when the heart is more active or the arterioles contract the blood-pressure rises, and that when the heart is less active or the arterioles dilate the blood-pressure falls. These factors also affect velocity. When the heart-beats increase in force, the velocity of the blood is increased ; when they are diminished the velocity is reduced. Further, it is obvious, from what has been said of the influence of the width of the vascular bed, that if the arterioles dilate the velocity of the blood through them is increased, and if they contract it is diminished.

In the pulmonary circulation the velocity is much greater than in the systemic, only one-fifth or one-sixth of the time being required for a lung circuit as compared with a body circuit.

Any attempt made to estimate the velocity of the blood by dividing an artery, and measuring the escape of blood from its cut end in a given time, would lead to erroneous conclusions, for the velocity in a closed artery and an open one are two different things. In the undivided artery the peripheral resistance reduces the velocity, in the divided artery the peripheral resistance largely disappears and the velocity is five or ten times greater, so that the carotid of a horse does not bleed with a velocity of 16 inches per second, but nearer 160 inches per second. Or, to put it in a practical way, if the carotid of the horse has a sectional area of 0·2 square inch, the amount of blood passing through the unwounded vessel amounts to 2 ounces per second, while if the same vessel be divided the loss of blood would be nearly 1 pint per second.

The **Duration of the Circulation** depends upon the length of time it takes a red corpuscle to travel from a given point and back to it again.* But there are many different paths it can take. For instance, from left heart through coronary vessels to right heart and again back to left heart would occupy a shorter time than a course through the liver, or through the feet or tail, so that a circulation time may mean nothing more than that a certain number of corpuscles have found the shortest cut through the circulation, or, on the other hand, have taken the longest. In a horse with a pulse frequency of 42, the average complete circuit is performed in 31·3 seconds (Hering), and is equivalent, according to the latter observer, to about 28 beats of the heart. In the rabbit with a pulse frequency of 168 per minute, the time occupied in completing the round of the circulation was 7·79 seconds, or, again, in 28 heart-beats; with the dog 16·7 seconds or in 26·7 heart-beats.

Stewart, who introduced the method of electrical conductivity for ascertaining the duration of the circulation, states that the time occupied by the blood in passing through the kidney, spleen, and liver is relatively long and much more variable than that in the lungs. In a dog weighing 13·3 kilogrammes the average circulation time in the spleen was 10·95 seconds, kidney 13·3 seconds, lungs 8·4 seconds. The same observer found the circulation time of the stomach and intestines of the rabbit to be comparatively short, not exceeding that of the lungs, while the retina and coronary vessels of the heart had the shortest time circulation.

Influence of the Nervous System.—It is only during the last sixty years that the existence of a set of nerve fibres governing the calibre of the bloodvessels has been known. C. Bernard observed that in the cervical sympathetic of rabbits there were fibres which on stimulation produced constriction of the bloodvessels of the ear; later he found a set of fibres which on stimulation produced a dilatation of the bloodvessels.

The control of the nervous system over the bloodvessels lies in these two directions—viz., dilatation and constriction; the nerves inducing the former are called *vaso-dilators*, and those bringing about the latter *vaso-constrictors*. Collectively both nerves are known as *vasomotor*. The vaso-constrictor fibres act by causing contraction of the muscular coat of the arterioles.

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* The circulation time is determined either by injecting an easily distinguishable salt into the blood, or more precisely by increasing the electrical conductivity of the blood by injecting into it a neutral salt solution.

The capillaries take no part; in fact, as far as is at present known, there is no vasomotor supply to capillaries. The vaso-dilators act by relaxing the muscular coat of the arterioles.

From what has been previously learnt it is evident that a high blood-pressure is an essential condition throughout the life of the animal; whether awake or asleep, at work or at rest, a constant watch has to be kept over the vessels of the body, in order to produce not only an effective but a purposeful circulation, for it is evident that the blood-supply to an organ in active secretion must be greater than when the organ is at rest. The nervous system is charged with the duty of controlling the bloodvessels, and has to regulate these matters automatically.

The system of nerves governing the bloodvessels is not under the control of the will, but belongs to that portion of the nervous apparatus generally known as the sympathetic. The sympathetic system has its origin in the brain and spinal cord; it is specially charged with functions relating to plain muscular tissue, cardiac muscle, and glands, so that the plain muscle constituting one of the coats of the arterioles comes under its control. The two opposite changes in the bloodvessels—viz., contraction and dilatation—are not brought about by the same nerves. The constrictor nerves operate through the elaborate and complex system to which they belong—viz., the sympathetic; but the dilator fibres accompany cranial and spinal nerves, and may or may not have any connection with the sympathetic system.

The **Constrictor Fibres** originate in the medulla at a special part known as the *vasomotor centre,* and the fibres from the centre pass down the spinal cord in that portion known as the inferior horn of the grey matter. At every segment of the spinal cord between the first dorsal and third or fourth lumbar vertebræ, these nerves flow out of the spinal canal in company with the inferior roots of the spinal nerves, and, leaving the latter, join the ganglia on the sympathetic, which lie just under the arch of the ribs.

The fibre which joins these constrictors to the sympathetic is the *white ramus communicans,* and it is spoken of as the *preganglionic* fibre. In the ganglion the fibre terminates, and a fresh cell in the neighbourhood of its termination gives rise to a new fibre, which leaves the ganglion and is spoken of as the *post-ganglionic* fibre or *grey ramus communicans.* This fibre is structurally different from the pre-ganglionic, for it is non-medullated, it passes back to the spinal nerves, and by entering the axillary and sacral plexuses reaches the bloodvessels of the limbs; those for the skin of the trunk pass by the corresponding spinal nerves.

This return path to the spinal nerves is not followed by the constrictor fibres which supply the bloodvessels of the head and neck. These come off at first from the thoracic roots of the spinal cord, and having passed through the vertebral sympathetic ganglion, they proceed to the inferior cervical ganglion, and by means of the cervical sympathetic gain the superior cervical ganglion. From this the constrictor fibres for the head issue.

The constrictor fibres to the bloodvessels of the abdominal viscera have another arrangement. They come out from the spinal cord as the greater and lesser splanchnics, and pass to the semilunar ganglion, in which the nerve enters and ends ; from the ganglion more non-medullated nerves issue, and pass direct to the vessels of the viscera.

The essential feature in all these constrictor fibres is that they originate in the brain or cord, leave the latter as medullated nerves, and enter a sympathetic ganglion, where they terminate by arborising around cells in the ganglion. From these cells new fibres arise, which leave the ganglion as non-medullated nerves, and proceed to their destination either direct, as in the head, neck, and viscera, or reach it through the spinal nerves.

If the spinal cord be divided below the medulla, and life maintained by means of artificial respiration, the immediate effect of division is a great fall of blood-pressure, due to dilatation of the bloodvessels ; in the dog it will drop two-thirds below the normal. The effect of division has been to cut off the constrictor influence, which was evidently issuing from some point above the section.

If in another animal the section be made above the medulla, no effect is produced on the blood-pressure. Evidently, therefore, the medulla contains a centre presiding over the important functions of maintaining the bloodvessels in the partially contracted condition known as *tone*, and it can readily be shown that this centre lies in the region of the fourth ventricle, and is only a few millimetres in length and still fewer in breadth. To this small area the name **vasomotor centre** has been given.

This centre, we have learnt, must be kept in a constant state of activity. This is effected, though perhaps not entirely, by the constant flow of impulses from the periphery to the centre. Impulses passing to a centre from without to within are known as *afferent*, those passing out from a centre to the periphery are spoken of as *efferent impulses*, and a collection of nervous matter where afferent impulses are received and efferent discharged is known as a *reflex centre*.

The afferent impulses which govern the centre in the medulla are carried to it through the spinal nerves from areas such as the skin and abdominal viscera, for these are the two great vascular areas which maintain and regulate the blood-pressure. On entering the superior root of the spinal nerves, the fibres travelling up the cord by means of collateral branches, make connection with the vasomotor centre in the medulla. We have now seen the channels by which this almost microscopic collection of cells in the medulla is brought into connection with the vessels of the whole body.

The impulses carried by afferent fibres to the vasomotor centre are of two antagonistic kinds ; they either stimulate it and produce contraction of the bloodvessels, with a consequent increase in blood-pressure, or they diminish the tone of the centre, produce a relaxation of the bloodvessels, and a fall in pressure. The first fibres are known as **pressor,** the latter as **depressor,** terms which correspond to the effect they produce on the blood-pressure.

As previously stated, it is in the skin and abdominal viscera that the impulses which regulate the maintenance of normal arterial pressure originate ; there are supplemental sources, but the above are the most important. The fibres passing from the skin area are stimulated by the external temperature, a low temperature causing impulses to be transmitted which contract the vessels, a high temperature causing a relaxation of the vessels, accompanied by congestion of the skin. But the splanchnic area is even more actively important than the skin in regulating blood-pressure, especially in those animals such as the herbivora, where the alimentary canal is largely developed. If the splanchnics be cut, the intestines become congested, in consequence of dilatation of the bloodvessels, and there is a severe fall in blood-pressure. If the peripheral end of the divided nerve be stimulated, the vessels contract, and the blood-pressure at once rises.

The action of the constrictor fibres of the bloodvessels is always more in evidence than that of the dilators, and the reason of this can be readily understood by remembering that the arterioles have always to be kept in a condition of contraction if blood-pressure is to be maintained.

Bernard's classical experiment of dividing the cervical sympathetic in the rabbit produces not only a remarkable picture of vasomotor effects, but illustrates the constrictor impulses which are constantly passing to the bloodvessels. On division of the sympathetic, the ear on that side suddenly becomes flushed with blood, hot, and congested, and vessels not previously visible to the naked eye now become very apparent ; and if the upper end of the nerve be stimulated, so as to imitate roughly the impulses passing along it in an intact condition, the vessels at once contract, the flushed appearance disappears, and the ear becomes cooler.

Since, in the above experiment, mere severance of the nerves which connect the bloodvessels with the central nervous system leads to a dilatation of the arterioles, it is evident that impulses are, under normal conditions, being continually sent out along the nerves from the vasomotor centres. These impulses keep the arterioles normally in that state of medium or partial constriction which has already been described as arterial '**tone**.' Now, inasmuch as the function of the vasomotor nerves is to regulate the blood-supply to any given area of the body, in exact accordance with the varying needs of that area, 'tone' becomes a factor of the utmost importance in this regulative mechanism. Without it all the arteries of the body would, in the ordinary passive condition of rest, be dilated to their full extent; hence no increased supply of blood could be provided except by an augmented activity of the heart, which would, of course, affect the body as a whole, and not any one limited part of it. 'Tone' insures that an arteriole may both dilate and contract, according as it receives less or more of the continuous constricting impulses, and thus the regulation of a varying blood-supply is made extremely perfect.

If the sciatic or brachial nerve be divided in the dog, as a rule the constrictor influence over the bloodvessels of the limb is lost, the foot-pads flush, and the feet rise in temperature. If the central end of the divided sciatic be stimulated, it is generally followed by a contraction of the bloodvessels and a rise in pressure. Occasionally the tone of the centre in the medulla is not raised but reduced, and dilatation of the vessels and a fall in blood-pressure results. This experiment suggests that most afferent nerves such as the sciatic carry both pressor and depressor fibres, and that the effects which follow experimental stimulation depend upon whichever set of fibres is most efficiently stimulated (Fig. 38).

The best example of a depressor nerve is one we have already studied under that name (p. 57); it is the only peripheral nerve the stimulation of which invariably reduces blood-pressure. This nerve, it will be remembered, is capable of regulating the work of the heart by taking off strain through the medium of the abdominal venous cistern. Stimulation of the depressor acts like division of the splanchnic—viz., the abdominal vessels fill with blood and the blood-pressure falls.

In spite of the enormous importance of the vasomotor centre in the medulla, experimental inquiry shows that if the cord be divided in the lumbar region the vessels of the hind-limb dilate and the blood-pressure falls; but if the animal be kept alive the blood-pressure probably returns to the normal, though it is once again lost by destroying the already divided cord. These results are explained by saying that the cord possesses **vasomotor subcentres**, and that, given time, these are capable of carrying on the work single-handed. It is even possible to carry the inquiry a stage further, and by destroying all nervous connection, isolate the vessels from their innervation; even then the vascular tone may be recovered, and it is supposed that it is developed in the wall of the vessel itself, possibly in response to the stimulating influence of variations in their internal blood-pressure.

It is possible that the nature of the stimulus conveyed by afferent nerves to the vasomotor centre may determine the nature of the reflex which follows, and this is considered probable from the fact that the electrical stimulation of muscle always produces a rise in blood-pressure, whereas the mechanical stimulation by rubbing always causes a fall. The effect of stimulating the divided sciatic was recently referred to as producing constriction of the bloodvessels and a rise in pressure; but if the sciatic nerve be cooled and then stimulated, exactly the converse effects are produced—viz., a dilatation of the arterioles and a fall in pressure. Not only are the results obtained dependent on the nature of the stimulus, but the state of the centre itself is of the utmost importance in determining the results of reflex vasomotor stimulation. When an animal is deeply under the influence of chloroform or chloral, the functions of the vasomotor

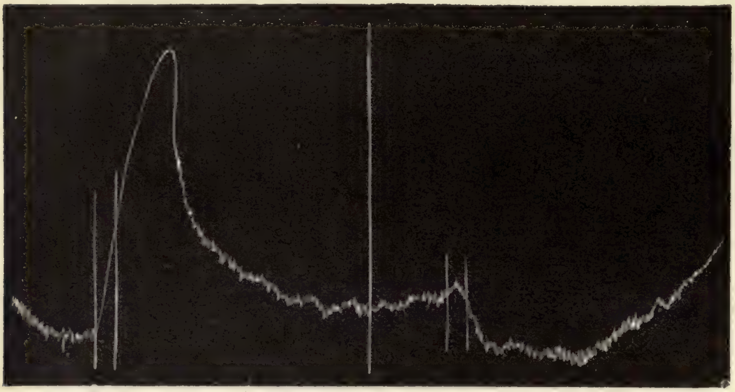

FIG. 38.—PLETHYSMOGRAMS: HIND-LIMB OF CAT (AFTER BOWDITCH AND WARREN).

To be read from right to left. On the left hand is shown the effect of slow stimulation of the sciatic (1 per second); on the right hand the effect of rapid stimulation (64 per second). In the first case the limb swelled owing to excitation of the vaso-dilators; in the second it shrank through excitation of the vaso-constrictors.

centre appear to be reversed, and excitation of *pressor* fibres causes a fall instead of a rise in pressure. If the centre be under the influence of strychnine, stimulation of the depressor nerve, instead of causing a fall in the general blood-pressure, produces a rise.

The vasomotor centres, both in the medulla and cord, are extremely sensitive to the varying amounts of carbon dioxide in the blood, and in this way they are believed to be capable of a good deal of self-regulation, apart from the afferent impulses which flow in to their aid. An increased venous condition of blood leads to a constriction of the arterioles and a raising of the blood-pressure. In asphyxia the arterioles remain constricted under the influence of the now intensely venous blood as it stimulates the vasomotor centre to unwonted activity, and though the initially high blood-pressure subsequently falls to zero, it does not do so because the arterioles have relaxed, but because the heart has failed.

It has been supposed that one cause of surgical shock is a deficiency of carbon dioxide in the blood. The prevention of this complication by avoiding a too free ventilation in the lungs, and so maintaining a carbon dioxide blood-pressure, has been recommended as a means of combating shock. The alarming depression which after a prolonged operation not infrequently follows the removal of the closed chloroform mask employed in chloroforming horses is doubtless due to the fall of blood-pressure caused by less CO_2 circulating in the vasomotor centre.

Rhythmical Activity of the Vasomotor Centre.—Under certain conditions, such as asphyxia and hæmorrhage, the vasomotor centre transmits to the vessels rhythmic constrictor impulses, which result in the appearance, on a simultaneous record of blood-pressure, of undulations, known as Traube-Hering curves (Fig. 39). They can, of course, only be detected by taking a tracing of the blood-pressure. The existence of these waves is indicative of abnormal excitation of the vasomotor centre.

The Dilator Nerves.—Hitherto we have mainly dealt with the constrictor influence exercised over the bloodvessels, but the nervous system likewise produces a *dilator* effect. In contrast to the constrictor influence, the dilator is not *tonic* in its action. It might be supposed that a dilator effect would naturally follow as the result of removing a constrictor influence from a vessel, without the intervention of a separate or antagonistic nerve supply; and this is exactly what does happen in most cases. But it is equally certain that special vaso-dilator nerves exist, of which the *chorda tympani* is one of the best examples. This nerve supplies the bloodvessels of the submaxillary gland with dilator fibres; if the nerve be cut no evident change in the bloodvessels occurs, but if the end in connection with the gland be stimulated the vessels dilate, the arteries throb, and the blood passes through the gland with such rapidity that the venous blood becomes arterial in appearance. Much the same phenomenon occurs when the *nervi erigentes*, through which erection of the penis is produced, are brought into activity. If these nerves be divided there is no effect, but if the peripheral end be stimulated the organ swells as the result of its enormously increased blood-supply, and the blood flowing through the dorsal vein may now be fifteen times greater in amount than in the quiescent condition.

Though it is clearly established that true vaso-dilator nerves exist, there is still a great difference of opinion as to the extent of their distribution. In most peripheral nerves, such as in the nerves of the limbs, both dilator and constrictor effects may, as has been mentioned, be obtained on stimulation, rapid induction shocks bringing about constrictor effects, slower shocks producing dilator effects. If the nerve—say the sciatic—be divided, the subsequent degeneration which follows affects the constrictor fibres earlier than the dilator. There is good reason for believing that the view originally held regarding muscles possessing dilator fibres may have to be modified in the light thrown on the matter by Bayliss, who has shown that there are fibres in the superior roots of the cord, where the axillary and lumbar nerves come off, which on stimulation produce dilatation of the vessels of the limbs. As these fibres are running from the limbs into the cord, difficulty has been experienced in explaining why stimulation should cause an impulse to

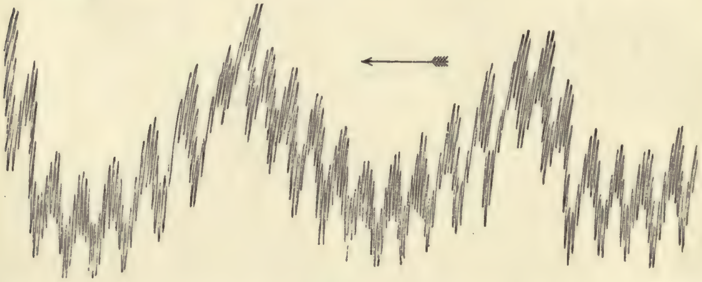

FIG. 39.—BLOOD-PRESSURE CURVE OF A RABBIT RECORDED ON A SLOWLY MOVING SURFACE TO SHOW TRAUBE-HERING CURVES (FOSTER).

The heart-beats are the closely situated up and down strokes, readily seen by means of a lens. The next curves are those generally regarded as due to respiration, the large bold undulations being the Traube-Hering curves. In each Traube-Hering curve there are about nine respiratory curves, and in each respiratory curve about nine heart-beats.

travel in a direction opposite to the normal. Such, however, is the only explanation at present offered—viz., that the fibres act in a double capacity, conveying to the cord sensory impulses from the limbs, and by the same fibres conveying efferent or outgoing impulses from the cord to the vessels, resulting in their dilatation.

The dilator nerves in their distribution—and we here refer to those whose existence is undoubted—behave very differently from the constrictor fibres. They leave the brain or cord by any cerebro-spinal nerve, and may or may not pass into a sympathetic ganglion before distribution. In contrast to the constrictors, they pass direct to their destination instead of taking a roundabout course, and they do not lose their medulla until near their termination. There is no positively known centre in the medulla governing the vaso-dilator fibres. There is, however, undoubted evidence of such a centre in the cord, for erection of the penis will still occur as a normal reflex after the cord has been divided above the lumbar region.

All the ‘ depressor ’ influences exercised on the circulation are not produced through inhibition (withholding) of constrictor impulses. Some must occur through stimulation of dilator nerves, but of this very little is positively known.

It is evident from what has been said that the knowledge of dilator nerves for the body tissues generally is still in a very uncertain condition.

We have seen the general effects produced by vaso-constrictor and vaso-dilator nerves, and indicated some of the gaps which exist in our knowledge. The broader features appear to admit of no doubt. The size of the vessels has to be automatically regulated according to the demand made for blood, so that a double set of fibres is provided, one to constrict and one to dilate them. A general contracted condition of the vessels must be maintained if the circulation is to continue ; consequently, constrictor impulses appear always more in evidence than dilator. These constrictor effects are assisted by the contractile reaction of the arterial wall, the result of the peculiar property of smooth muscle, and this contractile reaction is brought into play, even apart from nervous impulses, by the thrust given to the blood at each contraction of the heart. Substances circulating in the blood, the secretion of such glands as the adrenals, of which we shall learn more presently, act on the nerve plexus in the walls of the bloodvessels, constricting them and raising the pressure. The heart centre in the medulla is being constantly informed of what is occurring in the two vast systems—skin and splanchnic—which between them regulate the blood-pressure of the body. Equally, impulses are constantly streaming out from this centre to the vessels, some of a constrictor, others of a dilator nature, resulting either from the afferent impulses received or as the result of changes in the composition of the blood circulating through the medulla itself.

Absence of Vasomotor Nerves.—Some vessels have no vasomotor nerves. They have not been satisfactorily demonstrated in the vessels of the heart, nor in those of the lungs or brain. They are not found in veins (excepting the portal, which is really an artery), and are only provisionally accepted as occurring in muscles. If muscles possess vasomotor nerves, they must be essentially dilators, and it is easy to understand that these fibres may be brought into operation when the muscles contract, and thus provide a flow in proportion to the activity of the part. It has, however, been suggested that the dilatation in the bloodvessels of muscles during activity may be due to the chemical action of acid metabolic products on the vessels themselves.

Surgical Shock.—The condition known as shock, which follows certain operations, is intimately connected with the vasomotor apparatus. This has been suggested in speaking of the influence of carbon dioxide in the blood in maintaining blood-pressure. In surgical shock there is a marked depressor effect on the circulation, and a falling blood-pressure is one of the earliest indications of its onset. The maintenance of blood-pressure is the cardinal principle in combating shock, yet the physiologist does not regard shock as beginning in the vasomotor centre, as has been suggested, in consequence of the violence of sensory stimulation, but rather in the paralysis of the nervous connections with that centre. The cutting off of the afferent impulses which stimulate the vasomotor centre is the initial move towards the production of shock.

Aids to the Circulation.—The distribution of the blood supply in accordance with the requirements of the various organs is the special duty of the system of nerves we have been studying. The requirements vary from time to time, even from moment to moment. Active digestion diverts the blood to the splanchnic area ; active work causes the stream to pass into muscles, and later into the skin, in order to get rid of the excess of heat. Some glands, such as the kidneys, are secreting constantly ; others, like the pancreas, intermittently. A failing heart requires more blood, one struggling against an ever-increasing load requires less, and so on. Throughout the whole life of the animal this delicate balance has to be maintained, and it is effected by means of the nervous system through the medium of the heart and bloodvessels.

It is impossible in connection with this question of an efficient circulation to avoid once more referring to the heart, and it is impossible to avoid being struck by the close similarity in the nervous arrangement for the care, management, and control of these two communicating systems—heart and bloodvessels. The nerve fibres which constrict the bloodvessels, and those which cause a more forcible contraction of the heart, are of the non-medullated variety. They excite muscular action and increase wear and tear. The fibres which dilate the bloodvessels, and those which slow the heart, are both medullated, muscle-restraining, and exciters of repair rather than of disintegration. The impulses affecting heart and bloodvessels pass from the periphery to the centre—viz., they pass from skin and muscle, viscera and glands, and even from the heart and bloodvessels themselves, to the nerve centres presiding over these two important systems. They are true reflex effects, and without these impulses the centres themselves are powerless to effect regulation.

The delicacy of the balance must not be displaced. The body does not consist of a set of isolated functions working in sequence, three or four or a dozen may be in operation at the same moment, and to each of these a full blood supply must be guaranteed for so long and no longer than it is necessary, or in such reduced or increased quantity as may be needed. Awake or asleep, this remarkable give and take, this perfect adjustment to all requirements, is taking place from birth to death.

There has been reason to think that a certain amount of self-help has been obtained from the tissues themselves. For instance, the lactic acid and carbon dioxide formed during muscular activity may cause dilatation of the vessels and an increased blood supply. This chemical help has been for some time recognised, but it is only within recent years that we have learnt that the body is capable of elaborating substances which, when introduced into the blood, greatly affect the calibre of the bloodvessels and the rhythm and tone of the heart itself.

The Chemical Stimulus in Blood Supply.—The study of the so-called ductless and functionless glands of the anatomist has yielded one of the romances of physiology. The adrenals and pituitary bodies—tissues so insignificant in size that nothing more than a glance was rarely given them during dissection—are known to furnish to the blood-stream chemical substances of the utmost importance to the circulation.

An extract of the medulla of the adrenals, when introduced into the circulation, increases both the rhythm and tone of the cardiac muscle (see p. 59), and strongly stimulates the contraction of the arteries, excepting those of the heart, with a consequent great rise in blood-pressure. There is evidence that the internal secretion of the adrenals finds its way into the blood, for a larger amount of pressor substances may be recovered from the blood leaving the gland than from ordinary blood. Removal of the glands is followed by great weakening of the heart, low blood-pressure, and fatal results ensue.

Extracts of the posterior lobe of the pituitary body introduced into the circulation greatly increase the tone but not the rhythm of the heart muscle (see p. 59), and, with the exception of the kidney, it causes constriction of the arterioles of other parts of the body. This gland also secretes a depressor substance which diminishes the force of the heart and permits the vessels to dilate. Under experimental conditions the extract obtained from the pituitary body contains much less of the depressor than of the pressor substances, but it may well be that under physiological conditions they are passed into the circulation in the required proportion, and act, as in the case of the adrenals, as a direct chemical stimulus.

Muscular Aids.—Abdominal respiration assists the return of blood from the splanchnic area. If an incision be made in the posterior vena cava in front of the diaphragm, with every retreat of that muscle pressure is exercised on the abdominal contents, and the blood spurts out of the vessel. This pressure on the contents of the abdominal cavity is one of the most important mechanical aids to the circulation. The abdominal muscles are assisted by the stout elastic fascia which plasters their external surface, the anus is tightly closed, and the pressure within the abdomen is raised at each inspiration. Failure to secure this pressure results from a relaxed condition of the anus. This is frequently seen in the last stage of some debilitating diseases in the horse. The anus remains open, and allows the air to rush in and out of the bowel at every respiratory effort. In the veins of the hind-limb the whole course of the blood is directly against gravity until the posterior vena cava is reached. In that vessel gravity is in favour of the contents, for the vein falls from the spine to the heart, and the respiratory help above described completes the work as the heart is approached. The squeezing to which the liver is exposed in the abdomen is a most valuable means of assisting its circulation.

Muscular movements of the body and limbs are of the utmost importance as aids to the circulation. Muscles, by their contraction, squeeze the blood along the veins, regurgitation being prevented by the valves. Hill has shown that the column of blood in the vessels of the limbs may be broken up into segments, and by muscular action the stream turned on or cut off to a part, and the supply regulated according to its requirements. The importance of muscular action as an aid to circulation is seen every day, especially in the case of the horse. The swollen legs which result from standing are due to transudation, the result of the pooling of blood under the influence of gravity, and the absence of venous massage which results from muscular activity. We see it also in the feet, where the absence of exercise withdraws the needful stimulus from the circulation in the laminæ, and the feet become congested.

It is impossible for a man in an upright position to remain absolutely immovable. The slightest change in the pressure on the limbs brings muscles into play which force the blood along the veins. The same thing occurs in the horse, an animal that may not lie down for days or weeks together (and some *never* lie down). The weight imposed upon the hind-limbs is never equally distributed during repose. First one leg, then the other, takes the weight, and at every change in posture the muscles compress the veins and force the blood along. In the fore-leg these alternate changes in position are not necessary; the veins are short and near the heart.

The experiment of holding the domestic rabbit in the vertical position referred to at p. 71 is a good example of the manner in which the blood will pool under the influence of gravity in the absence of muscular support.

It is true that in the larger quadrupeds changes in posture are of a far simpler character than in the biped, the most frequent, perhaps, being that of the dependent head in grazing. This imposes a column of venous blood in the head and neck, from which it has to ascend against gravity. This is fully compensated by the venous cisterns beneath the masseter muscle, which at every masticatory act mechanically forces the blood into and along the jugular, the valves preventing regurgitation. In the days of bleeding, when jugular obliteration was not uncommon, such horses could not be grazed, owing to the vertebral veins being unable to compensate for the posture.

The left ventricle is capable of driving the blood throughout the entire vascular system, but it needs assistance. Under the conditions of a normal circulation it drives it principally as far as the arterioles, the skeletal muscles and valves in the veins afford the venous system the necessary support, and as the heart is approached the respiratory pump completes the emptying of the veins and fills the right heart.

Peculiarities in the Circulation through various tissues occur as the result of their special function. They are observed in the brain, erectile tissues, etc. The great vascularity of the brain necessitates that the blood should pass to it with a degree of uniformity which will insure the carrying out of its functions. It must never be left without blood, or immediate unconsciousness would occur. We see this provided for in the frequent arterial anastomoses—for example, the Circle of Willis and the Rete Mirabile of ruminants, which insures that not only does the blood enter with diminished velocity, but that if a temporary obstruction occurs in one vessel its work is readily performed by the others. The rete mirabile alluded to, which forms the arterial plexus on the base of the brain of ruminants, is considered by some to regulate the flow of blood to the brain when the head is depressed during grazing, and, it is said, accounts for the absence of cerebral hæmorrhage in these animals. It is probable that this may be one of its functions, but the horse possesses no rete, and his head is depressed during grazing for more hours out of the twenty-four than is the case with ruminants. It has probably, therefore, some other function to perform.

The free anastomoses of the vessels of the brain guarantee to it an uninterrupted blood-supply. In the dog both internal carotids and both vertebrals have been ligatured without causing unconsciousness or death, the supply of blood being kept up through the anterior spinal artery. The veins of the brain empty their contents into venous sinuses which from their structure are well protected from compression. There are no valves to the openings into the sinuses, nor are there valves in the thin-walled small veins of the brain.

The circulation in the brain is peculiar, inasmuch as its substance is contained within a closed unyielding cavity. A small space formed by the membranes exists between the skull and the brain, and in this is found a little fluid, which may pass into the interior of the brain or backward into the spinal canal. The cerebral fluid acts as a water-pad, and this fluid may be rapidly absorbed, for it readily passes into the veins at any pressure higher than that in the venous circulation. Nevertheless, the space which this renders available is very small, so that the brain may be regarded as incompressible. Special provision must, therefore, exist in its circulation to guard against a rise in blood-pressure, and this is furnished by dilatation of any one set of vessels producing a constriction of the other set. By this means no increase in size nor increase in blood capacity occurs; all that is affected is the velocity of flow. If the arterial pressure of the brain rises and that in the veins remains constant, there is an increased velocity of flow; if the arterial pressure is constant and the venous pressure rises, there is a diminished velocity of flow.

The brain presses against the cranium with a pressure equal to that in the capillaries. The brain-pressure, cerebro-venous pressure, and cerebro-spinal fluid pressure have been shown by Hill to be one and the same.

If the brain be exposed it is observed to rise and fall synchronously with the respiratory movements. Expiration causes the brain to rise by hindering the return of blood, while inspiration causes it to fall by facilitating its flow. Owing to the incompressibility of the brain substance in the cranial cavity the pulse is transmitted through the brain substance to the veins, and causes the blood to issue from them in pulses synchronous with the arterial pulses.

There is no vasomotor nerve supply proved to exist in the brain.

The singular arrangement of the venous plexuses of the corpus cavernosum penis admits of this organ attaining a great increase in size, a condition which in the brain every measure is adopted to prevent. The considerable size of the venous plexuses of the penis, their frequent intercommunication, the muscular pressure to which the veins leading from the sinuses are exposed, produce under the direction of the vasomotor nervous system a considerable increase in the volume of the part.

In some other organs the distribution of the bloodvessels is also peculiar. It is not known why the spermatic artery and plexus of veins should take such a remarkably tortuous course. Possibly, in some way or other, it may be concerned with the secretion of the glands, but its use is far from clear. On the other hand, tortuous vessels in the walls of hollow viscera, such as the stomach and intestines, perform a very evident function. We have only to think of the size of a collapsed and full stomach in the horse to recognise the necessity for some arrangement existing to prevent over-stretching of the vessels or interference with the blood supply.

The vast venous and arterial plexuses of the foot of the horse are a peculiarity in the circulation dealt with in the chapter devoted to the Foot.

Pathological.

A man is considered to be as old as his arteries, but a horse is as old as his feet and legs.

It is a remarkable fact that very little of the hard life of a horse falls on his arteries; with age the vessels become more rigid, but no sudden strain produces aneurisms, such as might be expected from the class of work performed; this is probably due to the fact that he does not suffer from syphilis. There is, however, one kind of strain which arises in the hunting field, or under similar circumstances, in which the walls of the external and internal iliac arteries suffer; in consequence of this a thrombus forms in the vessels which become partly or completely obliterated. Collateral circulation suffices in a state of repose, during which not a sign of any circulatory trouble is evident, but as soon as the animal gets to work sudden and painful muscular cramps occur, and finally temporary paralysis follows. These symptoms completely pass away with rest and return with work.

Parasitic trouble of the vessels is very common, the main seat being the anterior mesenteric artery, which is rendered rigid and aneurismal, and has its lumen obliterated by *Strongylus armatus*. It is remarkable how very little interference with the intestinal circulation occurs in consequence of this parasitic invasion, and it is equally astonishing how few horses are free from this infection. It is probably the most widely spread equine parasite.

Pulse.—The older physicians studied the pulse with care; at the present day it does not receive the same amount of attention. It is not sufficient to know the number of pulsations; the important point is the *character* of the wave.

A pulse may be *quick* or *slow*. Either of these may be *strong, weak, hard,* or *soft*. Strong and weak refer to the force of the ventricular contraction; hard and soft refer to the tension as judged by the finger—viz., the amount of pressure required to obliterate the pulsations. A further division of pulses is into *large* and *small*; this group refers to the volume of the artery. There is no pulse specially indicative of any given affection, but the *character* of the pulse in the prognosis of disease is of the utmost clinical value.

CHAPTER IV

RESPIRATION

SECTION I.

The Lungs.

The Chest Wall.—The chest is formed of a moderately rigid case furnished by the ribs and a flexible wall provided by the diaphragm. The contents of the chest are vascular and respiratory, and the provision made for their protection is not quite the same in each case. The vascular contents are mainly situated in the anterior portion, for here the heart is found with its bloodvessels, and relatively speaking only a small amount of lung. The horizontal spine of all animals throws upon the ribs a function not required in the biped. It would exceed the space at our disposal to deal with the peculiarities of the chest wall in all animals. That of the horse may be selected as a type, more particularly on account of its practical importance.

It is usual to speak of the ribs as true and false, but this conveys nothing as to their function. The true or sternal ribs form a case for the vascular organs, and help to support the horizontal spine. To enable this function to be performed they are shorter, stouter, and straighter than the false, or, as we would prefer to call them, respiratory ribs. Further, they are all inserted into the sternum either directly, as in the first pair, or indirectly by means of cartilage, as with the remaining seven pairs. The chest is very narrow between the two first ribs, but rapidly increases in width, as may be seen in the following measurements taken at the widest place between each pair in a riding-horse of medium height:

			Increase.
	Mm.	Inches.	Inches.
1st pair of ribs: greatest distance apart	90	3½	0
2nd ,, ,, ,, ,,	115	4½	1
3rd ,, ,, ,, ,,	160	6¼	1¾
4th ,, ,, ,, ,,	191	7½	1¼
5th ,, ,, ,, ,,	230	9	1½
6th ,, ,, ,, ,,	280	11	2
7th ,, ,, ,, ,,	355	14	3
8th ,, ,, ,, ,,	420	16½	1½
9th ,, ,, ,, ,,	470	18½	2

This table shows how rapidly the chest increases in width from front to rear, and the rate of that increase from rib to rib. If a vertical section of the chest be made—say between the fifth and sixth ribs—the thoracic cavity will be found egg-shaped, the broad part being above, the wall curving inward to obtain a hold in the sternum. From the first to the sixth rib the main function of the chest wall is to form a case for the vascular apparatus and to support the horizontal spine. The lateral movements of the sternal ribs is of no importance from a respiratory point of view. Some, like the first pair (Fig. 40), have no lateral movement, and it is very limited in the others, though it increases as we pass further back in the chest. Under forced respiration the fifth rib might take a limited share in respiration, but practically none of those anterior to it have any movement.

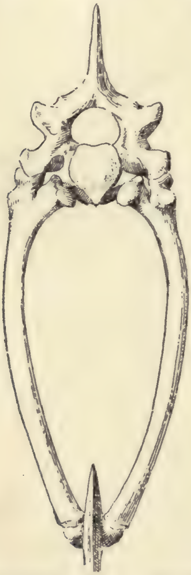

FIG. 40.—FIRST PAIR OF RIBS IN THE HORSE (AFTER SCHMALTZ: *Atlas d. Anat. d. Pferdes*).

It will be noted the way in which the head and tubercle are disposed in order to prop up the spine.

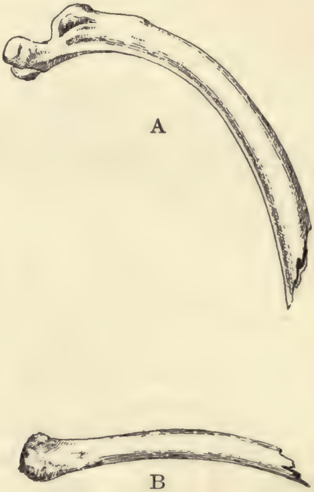

FIG. 41.—HEAD OF THE EIGHTH AND SIXTEENTH RIB OF THE HORSE (AFTER SCHMALTZ: *Atlas d. Anat. d. Pferdes*).

A is the eighth rib in normal position; the tubercle is still above the head. B is the sixteenth rib in position; the tubercle now lies behind the head, and cannot be seen from the front.

The relatively rigid cage formed by the first to the sixth ribs articulates with the spine, and it might be supposed that some rib movement favourable to respiration must occur, or the ribs would not form a joint with the spine ; but it may be suggested that this series of joints is of far more importance in securing flexibility of the spine than in respiratory functions, while the method by which they articulate shows that they are propping the spine up—a feature which is in marked contrast to the false ribs. If the true ribs be examined, it will be found that both the head and tubercle are large and well developed, the tubercle being disposed above the head (Fig. 41, A), and both so arranged towards the vertebræ that they prop it up. From the first to the seventh rib the substance and strength of rib is very evident ; from the eighth backwards the ribs decrease in size, both in width and depth, and the decrease in substance becomes progressively greater. From the first to the thirteenth rib the tubercle is above the head, but from the fourteenth backwards the tubercle is placed lower and lower, and finally is in the same horizontal plane as the head (Fig. 41, B). The tubercle begins to descend from the time the ribs are so far removed from the sternum, that no further propping up of the spine is possible.

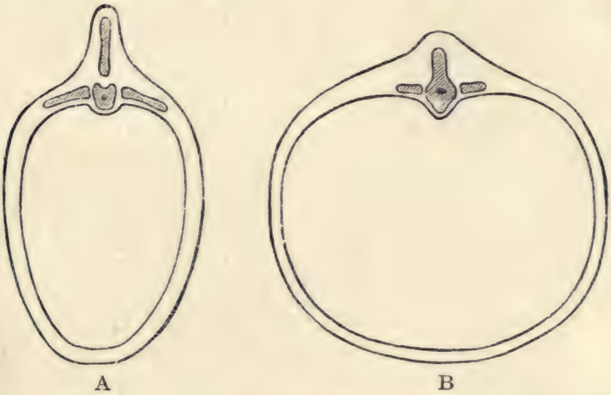

Fig. 42.—Vertical Section of the Body through the Eighth and Seventeenth Dorsal Vertebræ.

A, Eighth dorsal ; B, seventeenth dorsal section.

The narrowness of the anterior part of the thorax is to accommodate the fore-legs, which are, as it were, plastered on to it.

The false ribs have no sternal insertion, but each one is connected to the one in front by means of a piece of cartilage ; while rigidity of the walls is characteristic of the anterior chest, mobility is characteristic of that portion now being considered. The false ribs are narrow, thin, and curved. The curve gives the barrel shape to the side of the chest. Further, these ribs before they curve downwards have a relatively level or flat surface on their upper part, and on this the actual width of the back depends. From the ninth to the eighteenth the ribs decrease in length. The respiratory portion of the thorax extends from the seventh to the eighteenth rib. The movement of the ribs is mainly of two kinds. At their upper part they are partly everted and pulled forwards, below they are thrust outwards. The curvature of the rib is turned to account when it attempts the process of eversion, for by means of this movement very little eversion represents a distinct increase in the transverse diameter of the chest cavity. The semicircle formed by the cage is well seen in vertical section in Fig. 42, A and B, made at the anterior and posterior part of the thorax.

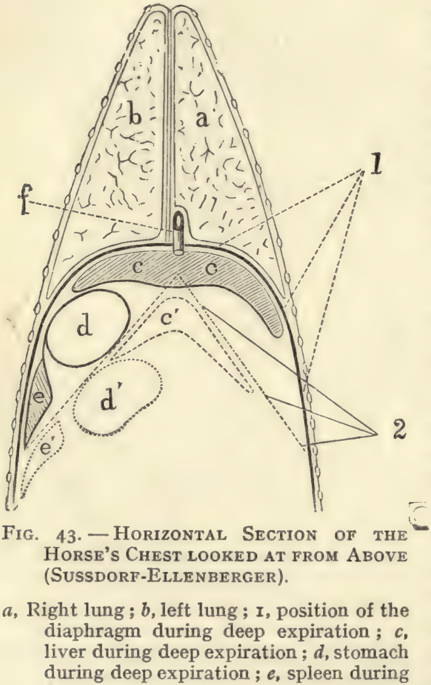

FIG. 43.—HORIZONTAL SECTION OF THE HORSE'S CHEST LOOKED AT FROM ABOVE (SUSSDORF-ELLENBERGER).

a, Right lung; *b*, left lung; 1, position of the diaphragm during deep expiration; *c*, liver during deep expiration; *d*, stomach during deep expiration; *e*, spleen during deep expiration; 2, position of diaphragm during deep inspiration; *c'*, position of liver; *d'*, of stomach; *e'*, of spleen during deep inspiration; *f*, posterior vena cava as it passes through the diaphragm.

A front to rear section of the chest (Fig. 43) is roughly egg-shaped, the narrow end of the egg in front, while the broad end is cut off obliquely for a considerable distance in the position occupied by the diaphragm. Of the latter we shall speak in detail presently, but it may be noted that the movements of the diaphragm and the other muscles of inspiration are capable during quiet respiration of lengthening the front to rear diameter of the chest by 10 to 12 cm. (4 to 5 inches), while at the widest part of the chest wall—viz., between the eleventh and twelfth ribs—the increase in side to side diameter is about 4 cm. (1½ inches).

Movements of the Diaphragm.—The vast musculo-tendinous sheet placed between the abdominal and thoracic cavities merits detailed consideration, owing to its importance in the respiratory mechanism. This muscle is placed obliquely forward in the body, and extends from the region of the loins to the sternum.

It roughly corresponds to the borders of the false ribs on both sides. In the right of its centre it is penetrated by the posterior vena cava; to the left and above its centre it is perforated to receive the œsophagus. Hung on to it are the liver wholly, and the stomach partly, and if it were not for two powerful tendons and muscles let into it from above, known as the cruræ, these weights could not be supported. Between the branches of the cruræ the posterior aorta escapes from the chest. The tendon of the diaphragm is centrally placed, and forms a dense feltwork of fibres, while the circumferential portion of the organ is muscular. The diaphragm is convex towards the thorax, resembling an open umbrella. This convexity is due to the pull exerted on it by the diminished pressure in the air-tight thorax, supplemented by the pressure of the abdominal viscera from behind. The diaphragm maintains its dome shape towards the thorax so long as the chest is air-tight. Even under pathological conditions, when the muscle is burdened by the effusion of gallons of fluid poured into the chest, no flattening of the diaphragm occurs.

The cavity of the chest is not cut off cleanly and sharply by the diaphragm. The central part of the latter is thrust forward into the chest, and by its projection it separates the two lungs at their posterior part, which in consequence rest on or wrap around the diaphragm, and as it were envelop it. The lungs, when fully distended, do not reach within 8 cm. (3 inches) of the cartilages of the false ribs. These points may be seen in Fig. 44, which gives a side view of the horse's chest. AFE indicates the margin around which the diaphragm is attached; the dotted line suggests the central part of the diaphragm thrust forward into the cavity of the chest on either side. This is covered by the lungs to within a short distance of the false ribs. If, therefore, the chest were punctured transversely anywhere below the dotted line in the diagram, and the instrument pressed through to the opposite side, the structure would suffer in the following order: lung, diaphragm, abdominal cavity, diaphragm, lung. To state these facts briefly, the largest respiratory area of the lungs lies on an obliquely placed dome-shaped table formed by the diaphragm, which projects into the chest.

The diaphragm recedes on inspiration, being pushed back into the abdomen, but the retreat does not occur evenly over its whole area. The central part of the diaphragm is naturally restrained by the posterior vena cava, the upper part and ribs move freely, while in the lower half—viz., from the vena cava to the sternum—the movement is again somewhat restricted. As the diaphragm recedes it compresses and carries back the whole of the abdominal viscera, more especially the liver, stomach, and spleen. The diaphragmatic curve of the colon is also carried back to a limited extent. But the chief result arising from the backward movement of the diaphragm is that connected with the circulatory system. Blood-pressure in the posterior vena cava is increased, the phrenic veins are emptied, and the portal vein is filled. The to-and-fro action of this muscle is a most important aid to the circulation. The limitation in movement of the central portion of the diaphragm suggests that no flattening of it occurs during inspiration, and this is supported by X-ray inspection in smaller animals. The viscera behind the diaphragm are affected by each of its backward and forward movements (see Fig. 43). The abdominal contents bulge forward, as it were, into the chest, and so behave, as has been described, like a piston being driven to and fro (see Fig. 45).

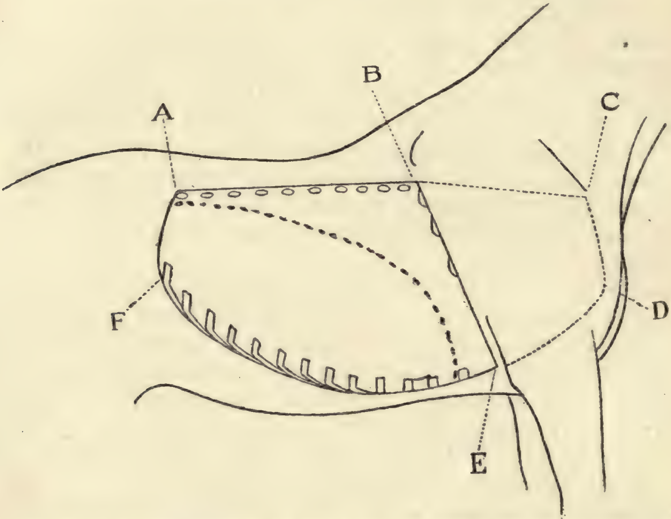

FIG. 44.—DIAGRAM OF THE EXTENT OF THE CHEST IN THE HORSE AND POSITION OF THE DIAPHRAGM.

The area B, C, D, E, is under the scapula and its muscles, and practically not available for auscultation ; the surface A, B, E, F, is the available area of the chest wall. The lung reaches to within a hand's breadth of the false ribs. A, F represents the last rib ; B, E runs parallel to the posterior edge of the triceps ; C, D corresponds to the position of the first rib.

The diaphragm bulges into the chest centrally, thus separating the two lungs. The curved dotted line falling from A to E represents the central line of the diaphragm, and shows the extent to which it encroaches on the chest.

The lungs contain more air during a deep than during ordinary respiration, so that the chest cavity is automatically reduced in size during an ordinary inspiratory effort in order to meet the

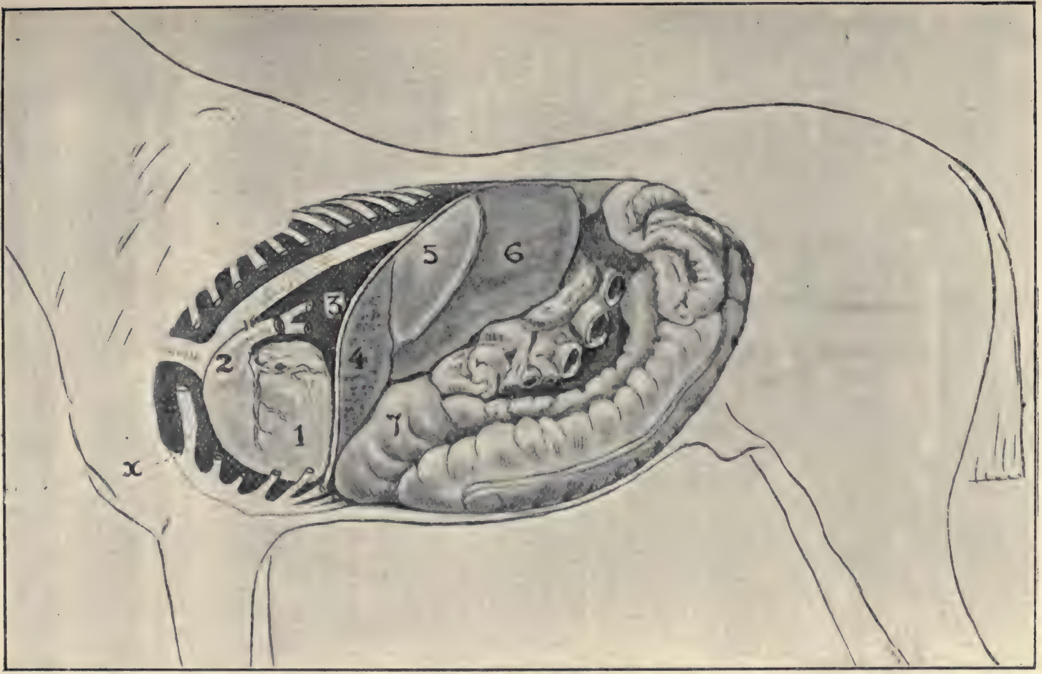

FIG. 45.—POSITION OF THE ABDOMINAL VISCERA AND DIAPHRAGM AT THE END OF EXPIRATION (AFTER ELLENBERGER AND BAUM: *Topographische Anatomie des Pferdes*).

1, The left ventricle; 2, pulmonary artery; 3, pulmonary veins; *x*, second rib. Note the oblique position of the heart in the chest, with its right ventricle inclining towards the sternum; also the suspension of the heart by means of its vessels. The encroachment of the central part of the diaphragm is well seen. 4 is the cut surface of the liver; 5, part of the greater curvature of the stomach; 6, the spleen; 7, the large colon. The pressure against the diaphragm is very obvious.

reduction in the amount of lung inflated. Fig. 46, taken from Ellenberger and Baum, slightly modified, shows the position of the lungs during normal inspiration.* The lungs are resting on the diaphragm, and it will be observed that this muscle may be seen passing to the ribs for attachment. During ordinary inspiration the portion of the thoracic cavity not occupied by the lungs is temporarily obliterated by the abdominal viscera being thrust forward, and thus pressing the diaphragm against the ribs and so closing the potential space. In Fig. 46, if the lungs were fully distended during the forced inspiration of work, they would extend to where the diaphragm is attached to the ribs, viz., about four inches above the edge of the false ribs. In Fig. 44, A, the dotted line under the loin indicates the limiting position of the lungs during a forced inspiration. During the ordinary inspiration of rest the dotted line would end further forward. The pressure behind the diaphragm can be realised by an inspection of Ellenberger's figures (Figs. 45 and 46). With this pressure against the diaphragm, especially during fast or heavy work, there is no difficulty in understanding why this muscle so frequently ruptures in the horse, and, as we shall see later on, it may help to explain the far more common lesion of ruptured stomach. During expiration Ellenberger represents the lungs as occupying a relatively very small portion of the thoracic cavity. His figure is not reproduced, as we think the space allotted to the collapsed lung is likely to prove misleading.

The Lungs Fill with Air.—Air is never absent from the healthy lungs, even after death. On life ceasing they retract, especially from the diaphragmatic region, and shrink upwards towards the spine. If they be now distended artificially, the organs gradually fill, those portions nearest the bronchus distending first. There is no sudden or unusual swelling, but rather a gradual invasion of different but neighbouring areas, which gradually come nearer and nearer together, and finally meet. The parts to expand last are the edges of the lungs and the surface in contact with the diaphragm, especially with its upper half. It is not intended to infer from these post-mortem observations that the distension of the lungs during life is identical, because during life they are never collapsed to the same degree, and, further, when distended after death, they inflate in the line of least resistance. Nevertheless, all parts of the lung are not equally distensible. The part situated around the roots of the lungs must necessarily, from the obstruction offered by the bronchi, be less distensible than those parts further removed. The anterior lobes, in consequence of the rigid nature of this part of the thoracic cage, can hardly move at all, though, of course, they are kept distended.

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* The writer's view is that the lung is not shown sufficiently distended.

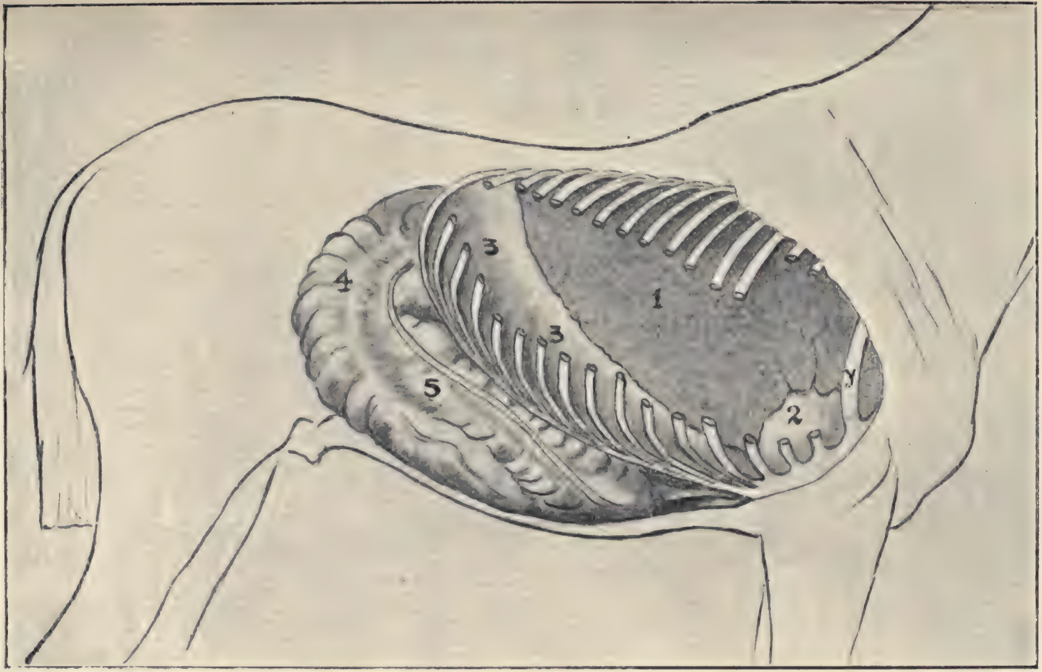

FIG. 46.—THE LUNGS, DIAPHRAGM, AND ABDOMINAL VISCERA IN POSITION DURING QUIET INSPIRATION (AFTER ELLENBERGER AND BAUM : *Topographische Anatomie des Pferdes*).

1, Right lung ; 2, the heart ; 3, the diaphragm ; 4, the large intestines ; *y*, second rib.

These drawings were made from frozen sections. We do not regard the lung as sufficiently distended even for a quiet inspiration.

The greatest amount of expansion occurs where there is the greatest amount of spongy lung-tissue and the least amount of bronchial ramification, and this necessarily exists in the outer zone of the lungs, particularly towards that portion facing the diaphragm, and corresponds to that part of the chest where the greatest movement occurs.

From this it must not be inferred that the lung in other places does not expand. As a matter of fact, the lungs fill up in the living animal every crevice not occupied by heart or vessel. There is no such thing as a pleural cavity in the healthy chest. The lungs lie close against the ribs, and never leave ribs or diaphragm during the whole life of the animal so long as health exists. There is, of course, a space between the costal and pulmonary pleura, but in health it is only a potential space. A finger introduced into the chest finds the lung close up against the opening which has been made, and if an attempt be exercised to inject fluid into the potential pleural sacs, the close application of the lung against the chest wall prevents it as effectually as it prevents a piece of soft rubber tubing from being passed along behind the costal and pulmonary surfaces. The lung exposed through this small opening may even bulge outwards under the pressure of the inspiratory act.

These facts must not be confused with those which may be observed under pathological conditions, when, the lungs having collapsed under hydrostatic pressure, as in the case of effusion into the chest, air readily enters the cavity through the cannula when the level of the fluid is lowered by tapping; for the lung is no longer in contact with the chest wall, having collapsed upwards towards the spine.

The areas affected in pneumonia might indicate which are the essential and which the non-essential portions of the lung in ordinary respiration. Pneumonia always affects the lower lobes of the lung, and nearly always the anterior lobes as well. The latter, owing to the curve of the spine, are on a lower plane than the upper lobes. It might be supposed from this that the upper part of the lung was of more respiratory importance than the lower, for with this surface of lung left the pneumonic patient can live for days. But in the upright animal the lower part of the lung is also the first in which pneumonia appears, and the lower part in the biped is the extreme upper part in the quadruped, from which it would appear that it is not necessarily the least efficient portion of the lungs in which pneumonia begins, though doubtless in the horse the least useful portion of both lungs is the anterior lobes.

The fact, however, remains that when air enters the lungs some parts expand much more than others. They do not behave like a bladder when being distended, but the largest amount of distension occurs where the greatest amount of spongy substance exists. This corresponds to the region where the greatest increase in antero-posterior and side-to-side diameters occurs. Though we have attempted to indicate that some parts of the lung are of more use than others, and that these parts are mainly filled during ordinary respiration, it must not be inferred either that the remaining portions are quiescent or that the lungs are firmly anchored within the chest. As a matter of fact, the roots of the lungs are carried back with each inspiration, and come forward at each expiration, and it is this which explains the up-and-down tracheal movement of the horse in hurried respiration.

A small hole into the pleural sac does not lead to collapse of the lungs even in the horse, but a large opening does. Even then the lungs continue to distend partly and retract, but only with difficulty, and finally asphyxia occurs. In all other animals in which no communication between the pleural sacs exist, the collapse of the one lung under the influence of a large opening into the chest is followed by the opposite lung doing extra work, and even bulging across the middle line of the chest in the mediastinal region.

In dealing with the distension of the lungs, the condition of repose has been assumed. If work be done, the respirations are increased. They are shorter and shallower, and may vary from 20 to 100 or more per minute, depending upon the nature of the work and the fitness of the animal. In such cases the lungs remain more fully distended than during repose, and the actual amount of air entering at each inspiration is less, owing to the fact that the respirations are more numerous, the rule being that when the rate of breathing is increased the depth is decreased.

Inspiration.—We have seen that during life the lungs occupy the whole cavity of a rigidly air-tight chest. So long as this air-tight condition is maintained, any movement which tends to increase the size of the chest causes distension of the lungs. By so doing, the air within them becomes rarefied, and thus a difference in pressure occurs between the outside air and that already in the lungs. In consequence, air rushes in to restore equilibrium, and this inrush is inspiration.

An increase in the size of the chest in its two diameters is caused by the movements of the diaphragm and the false ribs. The former retreats and carries with it the abdominal viscera, which are in consequence exposed to compression. The ribs generally are pushed outwards, while above they are drawn forwards, and their posterior edge everted, by which means the natural curve of the rib increases the side-to-side diameter. At the same time the intercostal spaces widen. By these means the capacity of the chest is increased, and the lungs at once fill the space thus created.

The tendency of the lungs is to recoil, owing to the highly elastic nature of their tissues, and the fact that they are normally in a state of distension. In the post-mortem condition they are much smaller than the chest. During life the chest cavity, being air-tight and larger than the lungs, the latter are distended by the atmospheric pressure within them.

During forced inspiratory movements the elbows are turned out, which brings auxiliary muscles into play, and allows a certain number of true ribs to take part in the chest movement.

Expiration.—The chest having been filled with air, the next process is its expulsion, and the mechanism concerned here is not entirely agreed upon by physiologists. At one time it was considered to be a purely non-muscular act, the elastic recoil of the lungs and of the abdominal muscles being the important factors ; but if the forward movement of the abdominal contents is to be credited with any influence in expiration, it is evident that the action of the abdominal muscles cannot be of the nature of an elastic recoil. There is some experimental evidence suggesting that a reflex nervous co-ordination exists between the inspirating muscles and the abdominal muscles, so that as the former cease to act, the antagonists at once come into operation. It will be shown later that this holds true of the muscles of locomotion, and there seems no reason why it should not apply to the muscles of inspiration and expiration. At any rate, the fact is undoubted that the contents of the abdomen travel chestward, and there seems no great reason why this should be brought about by the elastic recoil of the lung, and of the abdominal muscle, when a purposive movement, for which every facility exists, would be more to the point. As the abdominal contents are forced backwards in inspiration, the gaseous contents of the intestine are submitted to compression. This may be turned to useful advantage during the period of recoil. There is also the elastic recoil of the cartilages of the false ribs, seeking to return to their position of rest after inspiration ; but as material contributions to the effort of expiration, the two elastic recoils are not of any great value.

Expiration is considered by some physiologists as a passive act, and the view is partly based on the fact that it still continues after all nervous supply to the muscles is cut off. If the cord be divided below the origin of the phrenic nerves, all the muscles of the body posterior to the section are paralysed, but expiration still continues, due to the elastic recoil of the lungs.

Costal and Abdominal Respiration.—In the human subject two types of respiration have been described, one costal, as in a woman, and one abdominal, as in a man. It is now generally admitted that the costal type in the woman is an artificial condition, the result of compression. In the lower animals the breathing is essentially abdominal.

The **Fœtal Lung** contains no air, and therefore sinks in water. The first few inspiratory gasps at birth distend the alveoli, but for some time the conditions present in the adult—viz., the negative pressure in the pleural cavity, and the collapse of the lungs on opening the chest—are not found in the very young animal. They only occur when the cavity of the thorax is larger than the lung in a state of collapse. In the fœtus the lungs exactly fill the chest in the condition of expiration, and it is not until the chest cavity grows, as it were, too large for the lungs that a negative pressure in the thorax is produced. Later on (p. 138) the cause of the first act of breathing will be explained. Thoracic development in young animals is very rapid; a foal will increase 4 cm. (1½ inches) in circumference within the first few hours after birth; when this absolute increase in chest capacity is established, a negative pressure in the pleural cavity is obtained.

Muscles of Respiration.—The action of the muscles of the chest during respiration has been much disputed. The external intercostals doubtless, from the direction taken by their fibres, pull the ribs forward, and by so doing increase the transverse diameter of the chest; in this respect they are regarded as inspiratory muscles. The internal intercostals, the fibres of which run in an opposite direction to the external, draw the ribs backwards and act as muscles of expiration; and speaking generally, we may say that those muscles which draw the ribs forward are inspiratory, whilst those which draw them back are expiratory. The following table shows the inspiratory and expiratory muscles of the chest:

Muscles of Inspiration.	*Muscles of Expiration.*
Diaphragm.	Abdominal muscles.
External intercostals.	Internal intercostals.
Serratus anticus.	Transversalis costarum.
Levatores costarum.	Serratus posticus.
Serratus magnus (during laboured respiration).	Triangularis sterni.
Latissimus dorsi (during laboured respiration).	
Scaleni (during laboured respiration).	

In some animals the ribs do very little work and the diaphragm becomes the chief respiratory muscle. In most quadrupeds the sternum is fixed to the ribs and undergoes little or no movement; even the most powerful respiratory movements in the horse give rise to no sternal movement. On the other hand, there is a moderate amount of movement between the last two or three sternal ribs and the cartilages. During laboured respiration any muscle which can assist in advancing the ribs directly or indirectly is brought into play. This is well marked in dyspnœa.

After the expiratory act there is a pause before the next inspiration. In the horse at rest the period of expiration is as a rule longer than that of inspiration, though the proportion between the two is not invariable. During work the duration of the inspiratory and expiratory acts is about equal.

Intrapulmonic and Intrathoracic Pressure.—During inspiration a slight negative pressure exists in the trachea, and during expiration a slight positive pressure. A strong inspiration, with the glottis closed, such as can be made by a voluntary effort in man, rarefies the air in the respiratory passage and the pressure falls. Conversely a strong expiratory effort, with the glottis closed, as in coughing, defæcation, or parturition, raises the pressure in the respiratory passages considerably, and thereby increases the intrathoracic pressure. The increased pressure within the respiratory passages and thorax influences blood-pressure, for the veins leading to the heart are partly obstructed, as may be witnessed, for example, in man in a violent fit of coughing, and thereby the venous flow to the heart is lessened. In the pleural cavity a negative pressure is always present, due to the tendency of the elastic lungs to collapse. The value of this pull of the lungs on the chest wall has been ascertained for the sheep to be about 3 mm. ($\frac{1}{8}$ inch) of mercury, and during dyspnœa 9 mm. ($\frac{3}{8}$ inch). In the dog during inspiration the negative pressure in the pleural sac is 6 mm. ($\frac{1}{4}$ inch) of mercury, whilst during expiration 3 mm. ($\frac{1}{8}$ inch), has been observed. In the horse 6 mm. ($\frac{1}{4}$ inch) has been registered during a powerful expiration, and 28 mm. ($1\frac{1}{8}$ inches) during a powerful inspiration. The negative pressure can be recognised post mortem by the rush of air immediately the chest is punctured.

When the chest is opened during life, the atmospheric pressure within and without the lungs is equal, and in consequence the lungs shrink and in time collapse. In the horse a wound of the chest cavity is serious, for the reason that the two pleural sacs communicate, and therefore both lungs shrink and finally collapse. The collapse is not immediate, but gradual; the shrinkage is immediate. The collapse leads to death by asphyxia, unless the chest wound can be perfectly sealed, in which case the air in the chest cavity is absorbed, and the negative thoracic pressure restored. The remarks on this subject on p. 108 should be re-read.

The **Number of Respirations** varies with the class of animal; as a rule, the larger the animal the slower the respirations :

Horse	8 to 10 per minute.
Ox	12 ,, 15 ,, ,,
Sheep and goat	12 ,, 20 ,, ,,
Dog	15 ,, 20 ,, ,,
Pig	10 ,, 15 ,, ,,

Rumination increases the frequency of, and causes irregularity in, the respiration, and muscular exertion in all animals at once causes it to rise. In experiments on respiration this is most marked ; walking a horse will nearly treble the number of respirations, but the breathing begins to fall immediately the horse stops, though it does not reach the normal for a few minutes.

The ratio of heart-beats to respiration has been placed at 1 : 4 or 1 : 5.

The Effect of Respiration on the Circulation.—We have previously alluded to the influence of respiration on the circulation, and have pointed out that the negative pressure in the thorax assists the circulation by favouring the return of blood by the veins. This aspiratory action of the thorax mainly affects the anterior vena cava, but the contents of the posterior vena cava, we have seen, are also influenced during inspiration by the contraction of the diaphragm and the compression to which the vessels are exposed. These two important features have the effect of increasing at each inspiration the flow and velocity of the blood to the heart. Aspiration of the thorax favours the filling of the right heart, while the distension of the lungs in inspiration is generally believed to dilate the vessels, and so favour the flow of blood through these organs.

In dealing with the question of blood-pressure (p. 71), it was pointed out that the curve obtained shows certain undulations which are generally regarded as due to the influences of respiration, for it is found, if the blood-pressure and respiration curves be simultaneously obtained and superposed, that the undulations in the latter correspond very closely with the undulations in the blood-pressure. On comparing the curves, it is found that the blood-pressure rises with inspiration and falls with expiration ; further, it is observed that the rise does not take place immediately inspiration begins, nor does the fall occur immediately expiration starts, but shortly after in both cases, as may be seen in Fig. 29. These results have never been adequately accounted for ; but until the question was reopened by Lewis in recent years, the following was the explanation given of the respiratory rise and fall of blood-pressure.

If the curves be closely examined, it will be found that during inspiration the pulse frequency is increased, while during expiration it is decreased. This increase appears to hold good for all animals, and is considered to be due to a diminished activity of the cardio-inhibitory mechanism, while the reduction in pulse-rate is believed to be caused by a stimulation of the same centre. Any increase in the action of the heart results in more blood being thrown into the aorta, and so raises the blood-pressure, and this increase is supplemented by the aspiratory action of the right auricle in sucking in blood from the veins. So far, then, the general effect of a rise in blood-pressure during inspiration can be explained. The next thing to account for is the delay in the rise at the beginning of inspiration, and this is considered to be due to the dilatation of the lungs causing an increase in the capacity of the pulmonary vessels. The result of the increase is that they have to be filled, and the delay thus caused explains the delay in the rise of blood-pressure. In expiration the pulmonary vessels become smaller, and the delayed fall in pressure is attributable to these vessels having not yet returned to their expiratory capacity.

Such, then, is the explanation accepted by most physiologists, but in recent years the investigation of the phenomena by T. Lewis has resulted in considerable light being thrown on the matter. This observer shows that the respiratory curves of blood-pressure are of very complex origin, and unless the nature of the respiratory act be known, it is not possible to say what the effect on the blood-pressure will be. In a man trained to breathe with his ribs, the blood-pressure falls during inspiration and rises during expiration; when abdominal breathing is practised, there is a rise during inspiration and a fall during expiration; and with costal and abdominal respiration combined, intermediate results are obtained.

The secondary inspiratory rise of blood-pressure which follows the fall, where respiration is slow and the costal type of breathing is present, is, according to Lewis, due to lessened intrapleural pressure, therefore lessened pressure on the heart, and in consequence an increased filling of the organ. He was able to show, by introducing or withdrawing air from the pericardial cavity, how sensitive the heart is to an increase or reduction of intrapericardial, and therefore of intrapleural pressure.

The Nostrils.—Before the air reaches the lungs it is warmed by passing through the nasal cavities, so that it enters the trachea at nearly the body temperature. The incoming air also becomes saturated with watery vapour; this saturation likewise occurs in the nasal chambers. In the majority of animals air may pass either through the nose or mouth to enter the trachea, but in the horse, owing to the length of the soft palate, nasal respiration alone is possible; we therefore find in this animal the nasal chambers with their inlets and outlets well developed. The opening into the nostrils of the horse is large, funnel-shaped, and capable of considerable dilatation; it is partly cartilaginous and partly muscular. Immediately inside the nostril is a large blind sac, termed the **false nostril,** and one of its uses appears to be to increase the capacity of the nasal opening by allowing considerable and rapid dilatation. Another use is in the production of the peculiar snorting sound made by a horse either when he is alarmed or very 'fresh.'

During forced inspiration the nostril expands, especially the outer segment—viz., that part in communication with the false nostril—and the air is rapidly drawn up through the nasal chambers; during expiration the outer segment of the nostril collapses, but the inner segment, composed principally of the cartilaginous ala, dilates. Thus the movement of the outer and upper part of the nostril is principally inspiratory, of the lower and inner part mainly expiratory, producing a peculiar double motion of the nostrils well seen after a gallop or in acute pneumonia (Fig. 47). The dilatation of the inner segment of the nostril is brought about by muscular contraction and by the rush of expired air; striking the cartilaginous wing of the nostril, the current is directed outwards at an obtuse angle to its course down the nostrils, as may be well seen on a frosty morning when a horse is respiring rapidly.

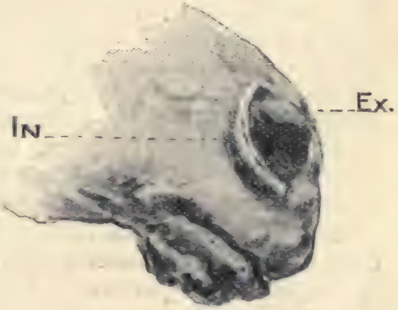

Fig. 47.—Nostril of Horse.

In, The inspiratory portion; *Ex*, the expiratory portion.

The nasal chambers are remarkable for their great depth and narrowness; the cavities are partly filled by the turbinated bones, which nearly touch the septum on each side, so that a deep but thin column of air passes through the chambers; the result of this arrangement insures that the air is saturated with vapour and raised to the proper temperature. The nasal chamber is divided into two parts, the lower or respiratory and the upper or olfactory. The latter will be dealt with under the Senses. It comprises the upper portion of the superior turbinated bone, ethmoid cells, and a portion of the middle meatus ; the respiratory channel, on the other hand, lies on the inferior part of the nasal chamber, and comprises the inferior meatus, inferior turbinated bone, part of the superior, and part of the middle meatus. The superior meatus may be said to be for the purpose of smell, the inferior for respiration, while the middle connects the sinuses of the face with the nasal passages.

The termination of the two turbinated bones and their connection with the external nostril is not as a rule fully described in anatomical works. The soft, fleshy appendix of the superior turbinated bone having divided and then reunited, is inserted into the cartilage of the nostril. In Fig. 47 the portion of the nostril marked *Ex* would have to be lifted upwards and outwards to see the seat of insertion of this bone. The lower turbinated bone also terminates in a fleshy appendix much larger than that of its neighbour. It divides: one branch is inserted into that portion of the nostril indicated *Ex* in Fig. 47, close, but external to, the appendix of the upper bone ; while the inferior division is inserted into the floor of the nostril. In order to see its insertion, the portion of the nostril *In* (Fig. 47) would have to be pulled outwards. The opening into the nasal chambers is formed, therefore, between the two fleshy terminations of the inferior turbinated bone, and in forced respiration these two divisions separate widely.

The Glottis.—The air having been warmed by passing over the septum and turbinated bones, enters the glottis, the arytenoid cartilages being separated to a greater or less extent to enlarge the opening. In quiet respiration this enlargement of the glottis is not very marked, but during work the cartilages are drawn powerfully upwards and backwards, and the V-shaped glottis fully opened (Figs. 54 and 56, p. 147). It is a remarkable fact that the laryngeal opening should be so relatively small, considering the diameter of the trachea and the size of the nasal openings.

During inspiration the larynx and trachea descend slightly, while they ascend during expiration. This is particularly well seen in horses during the hurried respirations of disease, producing a well-marked rhythmical movement of the laryngeal region and base of the tongue.

The Facial Sinuses are cavities in the face communicating with the nasal chambers ; they are of considerable size, occupying nearly the entire facial region, and they give the needful bulk to the head without adding to its weight; they are lined by a membrane which is continuous with that of the nose. These sinuses are filled with air which enters them through a foramen at the posterior part of the middle meatus ; during every act of respiration air is passing in or out of them. At first sight it would appear that air ought to enter the sinuses during inspiration, but the reverse is the case; it is only during expiration that they are filled, whilst during inspiration air is sucked out. Considering the position of the common inlet to these sinuses, it is difficult to understand why they should fill during expiration, though the advantage of hot instead of cold air entering is evident.

Respiratory Changes in the Air and Blood.—The changes which the air undergoes on passing into the lungs must now be considered.

ATMOSPHERIC AIR CONTAINS IN 100 PARTS AT 0° C. AND 760 MM. (30 INCHES)—

	By Volume.
Oxygen	20·96
Nitrogen	78·09
Carbon dioxide	00·03
Argon	00·94
Helium	Traces
Hydrogen	Traces

The proportion of carbon dioxide is small; it is a natural impurity in the air, though essential to plant life. The atmosphere also contains moisture the amount of which depends upon the temperature; the higher the temperature the greater the amount of water which the air can contain as vapour, and the lower the temperature the less the amount. Air may be dry or saturated, the latter term implying that it contains as much vapour as it can hold at the observed temperature; it generally contains about 1 per cent. of moisture, and is spoken of as dry if it contains ¼ per cent. The air which passes from the lungs is always saturated with moisture.

When air is taken into the lungs it alters in composition: it loses a proportion of its oxygen and gains in carbon dioxide, as may be seen in the following table:

	Nitrogen.	Oxygen.	Carbon Dioxide.
Composition of inspired air	78·09	20·96	0·03
,, ,, expired air	78·09	16·02	4·38
		−4·94	+4·36

The volume of oxygen absorbed is slightly greater than that of the carbon dioxide which takes its place, so that if dried and reduced to standard barometric pressure and temperature, the volume of *dry* air expired is slightly less than that of the air inspired. But since expired air is usually warmer than inspired (not always in the Tropics) and is saturated with aqueous vapour, the volume expired is actually greater.

Respiratory Quotient.—The proportion which the volume of oxygen absorbed bears to the volume of oxygen returned as carbon dioxide is termed the **Respiratory Quotient.** It shows the proportion of oxygen required to oxidise carbon, and is expressed as $\frac{CO_2}{O_2}$. The quotient on a *carbohydrate diet,* such as starch, is high, though rarely greater than 1, and generally about 0·9; for in starch the oxygen and hydrogen of the molecule exist in the proportion to form water, so that only the carbon remains to be oxidised. The quotient may, as has been said, be unity, or nearly so, depending upon whether the whole, or nearly the whole, of the O_2 is returned as CO_2. If a purely carbohydrate diet could support life, the R.Q. would be 1 exactly, as there would be as much of the O_2 returned as CO_2 as was taken in; for example—

$$\underset{\text{(Dextrose)}}{C_6H_{12}O_6} + 6O_2 = 6CO_2 + 6H_2O \quad \frac{6}{6} = 1.$$

On a *fat diet* the opposite condition exists: the fat molecule is poor in oxygen, and cannot supply from itself more than one-sixth of that required to oxidise the hydrogen to water; the remaining five-sixths have to be found from the incoming air, and in consequence less of the oxygen inspired is returned as CO_2. Thus:

$$\underset{\text{(Olein)}}{C_3H_5(C_{18}H_{33}O_2)_3} + 80O_2 = 57CO_2 + 52H_2O \quad \frac{57}{80} = 0{\cdot}71.$$

Consequently the R.Q. on a fat diet may be as low as 0·71. On a *protein diet,* which, in the matter of R.Q., comes midway between carbohydrate and fat, the oxygen in the molecule is still in insufficient quantities to oxidise its own hydrogen to water. It can contribute nearly half the amount required, but the remainder must be abstracted from the oxygen inspired. The R.Q. for protein varies, from circumstances which need not detain us here, but is generally taken at 0·8.

The R.Q. in animals depends, therefore, upon the nature of the diet: on one largely consisting of carbodydrates it approaches unity; on a diet of flesh it approaches that given for protein.

In herbivora the R.Q. is 0·9 to 1·0.
In carnivora the R.Q. is 0·75 to 0·8.
In omnivora the R.Q. is 0·87.

The value of the R.Q. lies in its being a measure of the oxidation occurring in the body as a whole. As a rule the amount of carbon dioxide formed is less than the oxygen absorbed, but there are exceptions, as in hibernating animals where the processes of oxidation are at their lowest point. In such cases the R.Q. shows the possibility of oxidation occurring without the production of carbon dioxide, and of carbon dioxide being formed without a sufficient absorption of oxygen to account for its production. Respiratory quotients as low as 0·3 have been found in hibernating animals, while during the period of their active life, when laying up or storing fat for winter use, the R.Q. may be greater than unity—even as high as 1·39. Such high quotients are not unknown among non-hibernating animals after a diet rich in carbohydrates, as in the case of fattening animals.

In these cases the carbon dioxide excreted is in excess of the oxygen absorbed. The carbohydrates are being stored up as fat, which is poor in oxygen; more oxygen is consequently rendered available for the food for the production of CO_2, which is split off from the carbohydrate molecule when converted into fat.

The R.Q. is not altered by muscular work, provided it is not excessive or carried to the point of fatigue (see Table, p. 141). More oxygen is absorbed and more carbon dioxide given off during work, but the ratio is the same as during repose. The inference from this is that the material which is being used up by the muscles both during rest and work is the same. With fatiguing work the R.Q. may fall, and this suggests that the body fat is being drawn upon.

In a starving animal the R.Q. diminishes, the creature lives on its own tissues, and as the body contains only a trifling amount of carbohydrate, it is on the fats and protein that the animal lives. During starvation the output of carbon dioxide falls off at a greater rate than the consumption of oxygen.

There are **other gases returned from the lungs** besides oxygen and carbon dioxide, but very little is known about them. Both **hydrogen** and **marsh gas** are given off in the expired air of ruminants, derived from the intestinal canal after having been absorbed by the blood. The amount has been placed at 3 litres (183 cubic inches) in twenty-four hours. The nitrogen of the air is returned unaltered.

Ventilation of the Lungs.—The lungs of an average horse contain, when fully distended, 42 litres (1½ cubic feet) of air, and at each inspiration 4 litres (250 cubic inches) are drawn in during a condition of repose. As the animal during repose breathes ten times a minute, the whole lung is ventilated about once a minute.

The column of air in the respiratory passages extends from the nostrils to the infundibular cavities. The air existing in the alveoli is spoken of as the **alveolar** ; it is the important air in respiration, and carries out the effective respiratory changes. From the air-sacs to the nostrils is the '**dead space**'—that is to say, it contains air which is for the time being functionless from a respiratory point of view. The amount of the 'dead space' has not been determined for all animals ; in man one-third of an inspiration fills it, while the remaining two-thirds goes to the alveoli. This proportion must necessarily vary in different animals, depending on the length of the head and neck.

The composition of the air in the respiratory passages is obviously not the same throughout ; it grows progressively poorer in oxygen and richer in carbon dioxide from nostrils to alveoli. During expiration the air from the dead space is the first to leave, and some of the alveolar follows. During inspiration the incoming air is diluted with that already in the lungs, and its chemical composition altered. If it takes a minute to ventilate the lungs—viz., to replace entirely the air they originally contained—it is obvious that though some of the inspired air may reach favourably placed infundibular cavities at once, the bulk can only reach it gradually. In man it is estimated that about one-eighth of the alveolar air is changed at each respiration. How far an ordinary inspiration travels it is difficult to determine. Under the most favourable circumstances some of the axial stream of the current might reach the alveoli, especially of the anterior lobes, but the bulk of it will get no further than the bronchi. Some of this may effect deeper penetration at the next inspiration, while some of it will be expelled unchanged. In the infundibula the air is changed by the process of diffusion.

The composition of the air in the alveoli of the lungs has for years been a difficult matter to determine, yet in order to explain pulmonary respiration this knowledge is essential. The air in the alveoli possesses less oxygen and more carbon dioxide than expired air, for, as we have previously seen, expired air is a mixture of alveolar and fresh air, the latter passing away at the beginning. The alveolar air at the end of the expiration, which lies between these two extremes, is the mixed air. The air at the end of the expiration represents that in the alveolar spaces, as it has come from where the actual passage of the oxygen into the blood and the carbon dioxide out of it has taken place, and in consequence a knowledge of its composition is of the utmost moment

Haldane, to whom we are indebted for a method of obtaining the alveolar air, shows that in man the percentage of carbon dioxide is almost constant for the same individual, while the oxygen percentages are liable to great variation. The mean amount of carbon dioxide in alveolar air is found to be 5·16 per cent. in men ; it was less in women. Later on we shall better appreciate the value of this constancy.

During fast paces the respirations increase in frequency, and as they do so they decrease in depth. The actual bulk of an inspiration is less during fast paces than during repose, though the total amount of air respired in a given time is very much greater owing to the increase in the number of respirations.

The influence of work on chest-ventilation in increasing the frequency and decreasing the depth of the respiration is dealt with on p. 139.

The Respiratory Exchange.—The respiratory exchange which takes place is of two kinds : an *external respiration* between the air and the blood through the medium of the lungs, and an *internal respiration* between the blood and the tissues. Both these are complex questions, and far from being settled.

We have seen that the air leaving the lungs has gained over 4 per cent. in carbon dioxide, and lost nearly 5 per cent. of its oxygen. The excess of oxygen absorbed over carbon dioxide produced is explained by the fact that oxygen is required not only for the purpose of oxidising carbon to carbon dioxide, but also hydrogen to water. In addition to the above changes, the expired air is found to be warmer than the inspired, and to be saturated with water vapour. This indicates a loss of body heat and likewise a loss of water. We have also learnt that in the alveoli of the lungs the composition of the air is not the same as in the dead space, and that in effect it contains more CO_2 and less O_2. It is in the alveoli that the blood gets rid of its carbon dioxide, and takes up its oxygen, and this process must be examined in some little detail.

The **Gases of the Blood** are oxygen, carbon dioxide, and nitrogen. These may be extracted from the blood in the vacuum of a mercurial pump, or more conveniently by chemically expelling the oxygen by means of potassium ferricyanide, and the carbon dioxide by means of tartaric acid, and estimating their amounts. The proportion of gases found is liable to considerable variation, depending on the condition of the animal, the vessel from which the blood is drawn, the activity of the tissues, and even the length of time elapsing between collecting and analysing the sample.

The gases of venous and arterial blood are necessarily different. The figures given in the following table are only convenient averages, and represent the gases in 100 volumes of blood, measured at 0° C. (32° F.), and 760 mm. (thirty inches) barometric pressure:

	Oxygen.	Carbon Dioxide.	Nitrogen.
Arterial blood - - -	20	43	1·2
Venous blood - - -	12	50	1·2

Blood, in passing from arterial to venous, loses 8 parts of oxygen and gains 5 parts of carbon dioxide, the nitrogen remaining unchanged. This as a broad general statement suffices, but for the purpose of ascertaining the respiratory changes in

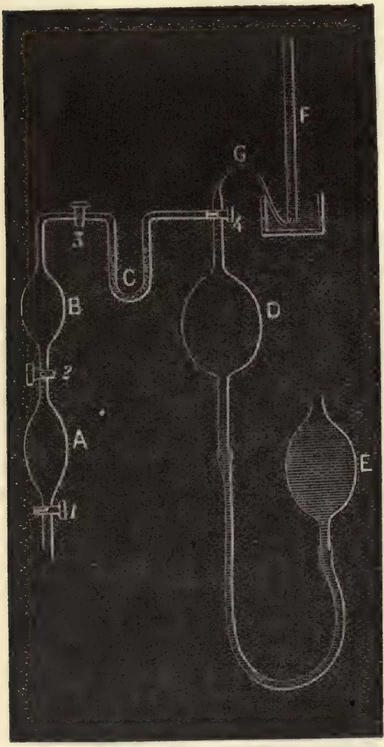

Fig. 48.—Scheme of Gas Pump.

A, The blood-bulb; B, the froth-chamber; C, the drying tube; D, fixed mercury bulb; E, movable mercury bulb connected by a flexible tube with D; F, eudiometer; G, a narrow delivery tube; 1, 2, 3, 4, taps, 4 being a three-way tap. A is filled with blood by connecting the tap 1 by means of a tube with a bloodvessel. Taps 1 and 2 are then closed. The rest of the apparatus from B to D is now exhausted by raising E, with tap 4 turned so as to place D only in communication with G till the mercury fills D. Tap 4 is now turned so as to connect C with D, and cut off G from D, and E is lowered. The mercury passes out of D, and air passes into it from B to C. Tap 4 is again turned so as to cut off C from D, and connect G and D. E is raised, and the mercury passes into D, and forces the air out through G, the end of which has not hitherto been placed under F. This alternate raising and lowering of E is continued till a manometer connected between C and 4 indicates that the pressure has been sufficiently reduced. The tap 2 is now opened. The gases of the blood bubble up into the froth chamber, pass through the drying-tube C, which is filled with pumice-stone and sulphuric acid, and enter D. The end of G is placed under the eudiometer F, and by raising E, with tap 4 turned so as to cut off C, the gases are forced out through G and collected in F. The movements required for exhaustion can be repeated several times till no more gas comes off. The escape of gas from the blood is facilitated by immersing the bulb A in water at 40° to 50° C.

the blood, the mixed venous blood of the body—viz., that found in the right ventricle of the heart—should be examined. An analysis of this, from the dog, compared with arterial blood, is given in the following table:

Venous Blood from Right Ventricle.			Arterial Blood.		
Oxygen.	Carbon Dioxide.	Nitrogen.	Oxygen.	Carbon Dioxide.	Nitrogen.
Mean.	Mean.	Mean.	Mean.	Mean.	Mean.
$11{\cdot}9\left\{\begin{matrix}16{\cdot}6\\5{\cdot}5\end{matrix}\right.$	$44{\cdot}3\left\{\begin{matrix}47{\cdot}5\\38{\cdot}8\end{matrix}\right.$	$2{\cdot}0\left\{\begin{matrix}4{\cdot}01\\1{\cdot}32\end{matrix}\right.$	$19{\cdot}2\left\{\begin{matrix}23{\cdot}3\\15{\cdot}0\end{matrix}\right.$	$38{\cdot}8\left\{\begin{matrix}43{\cdot}1\\34{\cdot}8\end{matrix}\right.$	$2{\cdot}7\left\{\begin{matrix}5{\cdot}50\\1{\cdot}62\end{matrix}\right.$

The mean and the extremes are shown in the above table, which gives a good idea of the variations in the amount of gases met with, especially in venous blood; and the same doubtless holds good for all animals. Both nitrogen and argon are found in blood. It is believed they are in simple solution and of no physiological value.

Oxygen in the Blood.—If the oxygen in blood were held in simple solution, as it is in water, and the blood introduced into a mercury pump, with every reduction in pressure in the pump oxygen would be given off from the blood. But in effect this is not so. It is not until the pressure in the pump stands at one-third of an atmosphere that oxygen begins to escape, and when the pressure is reduced to one-sixth of an atmosphere, the oxygen is suddenly and vigorously liberated. It is evident that its union with something has been suddenly broken, and this something is hæmoglobin. Further evidence that the oxygen is not simply absorbed by blood is afforded by the experiment of shaking air and blood, and oxygen and blood, together. The blood absorbs more oxygen from the air than an equal bulk of water would, while it absorbs no more from an atmosphere of pure oxygen than it does from atmospheric air. The explanation is that the oxygen and hæmoglobin form a definite chemical compound.

The oxygen in blood is carried in two forms: a very small quantity, amounting to 0·65 volumes per cent., is simply dissolved in the plasma; the other and larger portion is the oxygen chemically combined with hæmoglobin, which may be conveniently taken at 20 volumes per cent. Oxyhæmoglobin possesses the property of giving off its oxygen when the pressure in the surrounding medium falls sufficiently low. We have already seen this occur in the blood-pump.

The process is termed **dissociation**; this may be defined as the tendency which certain gases have to leave the substances with which they are united when the surrounding pressure becomes reduced. In the animal body it is not confined to the combination of oxygen with hæmoglobin; the same process is at work in assisting to liberate the carbon dioxide in the lungs from the substances with which this is chemically combined.

When sufficient hæmoglobin exists in 100 volumes of blood to carry 20 c.c. of oxygen, the hæmoglobin is said to be saturated. If only half the amount exists, then only 10 c.c. of oxygen are in chemical combination in 100 c.c. of blood, and the percentage of saturation is 50. Two dissociation curves are given in Fig. 49, one for horse's blood, and one for a solution of dog's hæmoglobin. The curve illustrates the blood-pump experiment previously described. At 150 mm. pressure of oxygen, corresponding to atmospheric pressure, the blood is saturated with oxygen. It contains 20 c.c. in each 100 volumes. In horse's blood there is no attempt at dissociation until the pressure is reduced to 50 mm., and by the time it has fallen to 14 mm. half the total amount of oxygen united to the hæmoglobin has

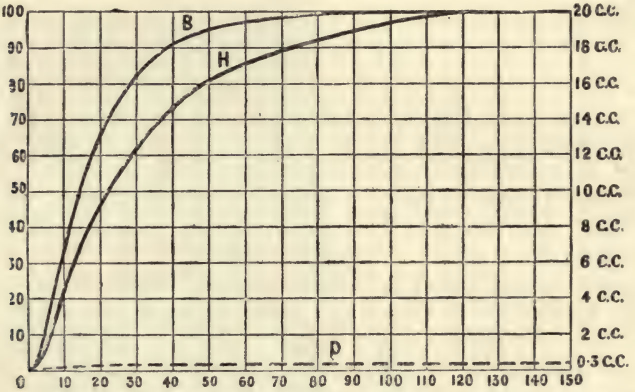

FIG. 49.—CURVES OF DISSOCIATION OF OXYGEN FOR HORSE'S BLOOD (B) AND DOG'S HÆMOGLOBIN SOLUTION (H) AT 38° C. (BOHR).

Along the horizontal axis are plotted the partial pressures (numbers below the curve) of oxygen in air, to which a solution of hæmoglobin was exposed. The corresponding percentages of oxygen are given above the curve. Along the vertical axis is plotted the percentage saturation of the hæmoglobin with oxygen. Thus, on exposure to an atmosphere in which oxygen existed to the extent of 1 per cent., corresponding to a partial pressure of 7·6 mm. of mercury, the hæmoglobin took up about 75 per cent. of the amount of oxygen required to saturate it. When the oxygen was present in the atmosphere to the amount of about 10 per cent., corresponding to a partial pressure of 76 mm. of mercury, the quantity taken up by the hæmoglobin was about 96 per cent. of that required for saturation.

dissociated. Below 14 mm. the remaining half is given off rapidly and suddenly.

Arterial blood enters the capillaries with 20 volumes of oxygen per cent. at a partial pressure of 100 mm. It leaves the tissues a second later with only 12 volumes of oxygen, having yielded up 8 volumes, or 40 per cent., of its original amount, in consequence of the fact that the partial pressure of oxygen in the tissues is practically nil. Dissociation of the hæmoglobin in the tissues has therefore occurred, and there is evidence to show that this is assisted by the presence of carbon dioxide.

Taking advantage of the fact that only a trifling percentage of the oxygen in blood is dissolved, while the bulk is chemically combined, Haldane was able to show that the oxygen capacity of the blood varied with the colouring power, and thus established a method of clinically estimating the hæmoglobin in any sample.

Carbon Dioxide in Blood.—This gas is held in blood both in simple solution and in chemical combination, the latter accounting for the larger part of the contained gas. Two-thirds exist in the plasma, and one-third in the corpuscles. In a gas-pump the blood gives up all the carbon dioxide it contains; but if, instead of using blood, serum be so extracted, it is found impossible to obtain the whole of the carbon dioxdie from the latter without the use of an acid. This notable difference between the blood and serum suggests that the hæmoglobin of the red corpuscles acts like an acid, and breaks up the compound containing the carbon dioxide. It appears according to the most recent views that a portion of the carbon dioxide is held as sodium bicarbonate, and another portion in an organic combination. The latter is probably furnished by the protein of the plasma on the one hand, and by combination with hæmoglobin on the other, for hæmoglobin has been shown to be capable of forming a weak compound with carbon dioxide.

It is believed that as the organic combination of carbon dioxide is more readily dissociated than the other, it is this part which does the main work in collecting the CO_2 in the tissues and liberating it at the lungs. The carbon dioxide carried by hæmoglobin is believed to be united with the protein portion of the molecules, thus leaving unaffected the iron moiety by which the oxygen is carried.

Circumstances influencing Respiratory Exchange.—Respiratory exchange is influenced by food, being not merely increased as the result of the considerable muscular effort involved during mastication, but directly excited by the nature of the food. Thus maize causes in horses a greater excretion of carbon dioxide and absorption of oxygen than an equal weight of oats. A protein diet causes a larger respiratory exchange than one of carbohydrate or fat. Respiratory exchange is greater in the young than in the old, less during sleep than when awake, greater in warm-blooded than in cold-blooded animals, greater in small than in large animals, and greater at work than at rest. Some of these points will be examined at length in the chapter devoted to their consideration.

Gaseous Exchange in the Lungs.—There are two theories put forward to account for the transfer of oxygen from the external air to the blood, and the passage of carbon dioxide from the blood to the external air. The first and oldest view is a physico-chemical one. If the partial pressure of the oxygen in the air cells is higher than it is in the blood, oxygen will pass into the blood.

If the pressure of the carbon dioxide in the blood is greater than it is in the alveolar air, carbon dioxide will be given off to the latter. Until recent years the acceptance of this explanation had been very general. When, however, the air in the alveolar cavities was examined, facts were discovered which threw grave doubt on the accepted view. It was found by certain observers that the pressure of oxygen in the arterial blood might be above that of the oxygen in the alveoli, and that of the carbon dioxide in the blood might be below the pressure of that in the pulmonary alveoli. Under these circumstances it was obvious that the theory of diffusion was no longer able to explain the respiratory exchange in the lungs, and a fresh explanation had to be found. The view held by those who reject the physical theory is that the respiratory exchange is carried out by a process of secretion, and this in the present state of our knowledge of physics and chemistry is very difficult to explain. We must look at both views more closely.

The picture of the diffusion theory is outlined above. The blood, robbed of 40 per cent. of its oxygen in the tissues, and carrying over 16 per cent. increase of carbon dioxide, makes its way back to the lungs in a partially reduced condition. Here it circulates through the vast capillary system spread over the alveoli of these organs, and is brought as closely as possible into contact with the alveolar air in the ultimate air-passages. Nothing but the capillary wall and the delicate moist membrane of the alveolus separates the blood from the air, and through this wall the oxygen instantaneously passes, in consequence of its partial pressure in the blood being low and that in the alveoli high. In the blood it is taken up by the plasma, and then absorbed by the hæmoglobin of the red cells, with which, as we have already seen, it forms a weak chemical compound. Concurrently with this, carbon dioxide, by the process of diffusion, passes out of blood in which its partial pressure is high, into the air of the alveoli, where the partial pressure is low.*

We have said that for some time past the law of diffusion and chemical dissociation has been held inadequate to explain the pulmonary exchange, the reason being that there are many observations, none of which, perhaps, are entirely free from error, which go to show that the alveolar air may contain a higher partial pressure of carbon dioxide than is found in the blood, while the oxygen tension of the alveolar air is below that of the blood. Under these circumstances diffusion is out of the question, and the only explanation which can possibly account for oxygen passing into the blood and carbon dioxide passing out of it is that which attributes these to a secretory activity.

It is no part of a work of this character to examine the rival physical and vital theories of pulmonary respiration, but no matter how difficult it may be to explain the secretion of oxygen, the fact remains that, reasoning by analogy, there is no difficulty in understanding the secretion of oxygen by the cells of the alveoli.

The so-called 'swim bladder' of deep-sea fishes contains a high percentage of oxygen. Cods brought up from a depth of 45 feet have shown 52 per cent. of oxygen in their gas reservoir, and gas drawn off on succeeding days has shown 79 per cent. and 84 per cent. of oxygen in the bladder. The production of this gas by secretion is the only possible explanation of its existence. As a matter of fact, there is a vascular area in the swim bladder from which it is formed ; and to render the secretory theory more complete, nerves supplied by the vagus have been found, which on section prevent the further accumulation of gas.

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* If a mixture of gases be absorbed by a fluid, it is found that the volume of each gas forming the mixture is absorbed as perfectly as if it were the only gas present ; no more and no less is absorbed, whether the gas be by itself or whether it form only a proportion of the mixed gases present. This is explained as resulting from the fact that one gas does not exercise any pressure upon the other gases with which it forms a mixture. The term used by Bunsen to define the pressure exerted by one gas in a mixture of gases is '*partial pressure.*' For example, 100 volumes of air contain at freezing-point 0° C., and standard barometric pressure 760 mm. (30 inches), 21 volumes of oxygen and 79 volumes of nitrogen. What is the partial pressure exerted by each gas in this mixture ?

$\frac{760\times 21}{100}=159\cdot 6$ mm. (6·3 inches) of mercury, which is the partial pressure of the oxygen ;

and

$\frac{760\times 79}{100}=600$ mm. (23·7 inches) of mercury, the partial pressure of the nitrogen.

The term 'partial pressure' occurs so constantly in all discussions of the nature and causes of gaseous exchanges of the animal body, that the above may help to make the matter clear.

In the researches of Haldane and Priestly previously alluded to the alveolar air was found to contain a remarkably constant percentage of carbon dioxide. This constancy is maintained by the increase in alveolar ventilation, which results from the increased production of carbon dioxide. The respiratory centre, these observers say, is exquisitely sensitive to the slightest increase in the alveolar CO_2 pressure, a rise of 0·2 per cent. of an atmosphere being sufficient to double the amount of alveolar ventilation during rest. It is an astonishing fact that the lungs should be able to arrange for their effective ventilation.

Internal or Tissue Respiration.—This is infinitely more obscure than pulmonary respiration—in fact, the means by which the tissues utilise the oxygen given to them is quite unknown.

We have previously seen that in the passage of blood through the capillaries of the tissues it loses in about one second 40 per cent. of its oxygen. This loss occurs in consequence of the dissociation of the oxyhæmoglobin in the presence of tissues whose oxygen tension is practically *nil*. The blood, when it left the pulmonary capillaries, was nearly saturated with oxygen—perhaps 19 c.c. of oxygen for every 100 c.c. of blood, equal to a partial pressure of 100 mm. of mercury. In the tissue, the oxygen being built up into living substance as fast as it is supplied, its partial pressure is *nil*. Under these circumstances, there is no difficulty in accounting for the transfer of oxygen from the blood to the tissues on purely physical and chemical grounds, the dissociation of hæmoglobin being in all probability assisted by the presence of carbon dioxide in the tissues, for, as previously mentioned, it is known that an increased tension of carbon dioxide in blood favours the giving up of oxygen to the tissues.

In consequence of the above changes, it is evident there is a reduction in oxygen tensions from the blood to the tissues; being highest in the blood-cell, it is less in the plasma, still less in the vessel wall, lower in the lymph, and at its lowest in the tissue elements. In fact, these various tissues deal with the hæmoglobin in order to obtain its oxygen, exactly as we deal with it outside the body in order to obtain its gases—viz., expose it to reduced pressure, as, for instance, in a mercurial pump. The blood, as we have mentioned earlier, does not give up all its oxygen in the tissues, probably on account of the rapidity of its passage. At no period, excepting under the condition of asphyxia, is the whole of the hæmoglobin reduced. There may be more oxygen returned to the lungs unused than has been abstracted by the tissues.

The whole of the carbon dioxide in blood is not got rid of in the lungs; that remaining in arterial blood on leaving the pulmonary capillaries is equal to 5 per cent. of an atmosphere or 35 mm. of mercury. On the other hand, the pressure of carbon dioxide in the tissues is high—50 mm. to 70 mm. In consequence, there is no difficulty in explaining on physical and chemical grounds the transfer of carbon dioxide from tissues to blood.

The medium in which this transfer occurs is the lymph which bathes the tissues. This is the carrier between the blood and the cell, for it is in the cell that tissue respiration occurs, and not in the blood.

As evidence of the important fact that the oxidations take place in the tissues, and not in the blood, two interesting experiments may be quoted. If the blood in a frog's body be replaced by saline solution, and the animal kept in an atmosphere of pure oxygen, it will continue to produce carbon dioxide. It is obvious in this case that the CO_2 has been produced from the tissue, as the animal is without blood. A more telling experiment is the following: Methylene blue is a comparatively stable oxygen-holding substance—more so than oxyhæmoglobin—and is likewise an extremely powerful dye. If a solution be injected into the circulation and the animal destroyed, the blood is found dark blue in colour, but the tissues, especially the muscles, are normal in appearance. When, however, they are exposed to the air, they turn a vivid blue. The explanation is that the tissues robbed the methylene blue of oxygen, and formed a colourless reduction product, which on exposure to the air took up oxygen and again formed methylene blue. No more remarkable example of the instantaneous absorption of oxygen by the tissues could be furnished.

In spite of the imperative necessity which exists for oxygen, it is remarkable how little can be obtained from the body. From muscle none can be obtained; from the various secretions—lymph, bile, urine, milk, saliva—only a very little can be obtained, though in all these cases there is an abundance of carbon dioxide.

In the respiration of muscle, which can be readily studied, the muscle preparation of a frog will go on contracting until exhausted in an atmosphere of hydrogen, producing carbon dioxide, thereby showing that it is using oxygen, yet neither in the muscle nor in the atmosphere surrounding it does any oxygen exist. The question, therefore, is, How does the oxygen-free muscle obtain oxygen for the production of carbon dioxide? Few things in the whole range of physiology are more difficult to understand, but it is supposed that when the oxygen reaches the muscle it is at once stored up in some compound or compounds among the muscle molecules; hence this substance has been termed intramolecular oxygen. It there loses the properties of free oxygen, and forms a complex substance which readily yields carbon dioxide and other matters on decomposition, and this passes into the bloodvessels of the muscle and is carried away to be got rid of at the lungs. The changes which the oxygen undergoes from the time it leaves the blood until it reappears as carbon dioxide in the tissues are completely unknown. It has been suggested that the nature of the oxidative changes occurring in living tissues may be due to the presence of oxidising ferments in the body—*oxydases*, as they have been termed. Such ferments have been demonstrated to exist in nearly all the tissues.

The phenomena of tissue respiration may be studied in living tissues by ascertaining the composition of the blood before and after circulating through them. Such an experiment has been carried out on the horse by Chauveau and Kaufman, utilising the levator muscle of the upper lip during feeding. The consumption of oxygen and the production of carbon dioxide was many times greater during activity than during rest. Glands such as the submaxillary have been similarly examined, while the respiratory changes occurring in the lungs during rest and work have formed the subject of many experiments. All tell the same story, though not all in the same degree. One remarkable example of this is furnished by L. Hill's examination of the respiratory exchange in the living brain, which, compared with skeletal muscle, was found to be very low.

It is impossible here to examine further the question of respiration in the tissues, but the question will be referred to in detail when its importance warrants it, as in respiratory exchange, muscular work, animal heat, and general body metabolism.

Deficiency in Oxygen.—When an animal is compelled to breathe the same air over and over again, there is a gradual loss of oxygen and an increase in carbonic acid, and though death will ultimately ensue unless the air be renewed, it is remarkable that before this occurs nearly the whole of the oxygen will have been consumed from the atmosphere. This is further evidence, if any be needed, that the oxygen is not simply absorbed by the blood, and that its absorption does not obey the ordinary laws of pressure. Experimental inquiry has proved that animals may live in an atmosphere containing only 14 per cent. of oxygen, that distress appears at 11 per cent., for at or below this pressure the hæmoglobin cannot take up its full amount of oxygen, and rapid asphyxia follows when the oxygen falls to 3 per cent.

In poisoning by carbon monoxide, the latter gas turns the oxygen out of the blood-cells, yet although the whole of the red cells are converted into carriers of carbon monoxide, the animal may still be kept alive in an atmosphere of pure oxygen under pressure, the amount of oxygen dissolved by the plasma at an oxygen pressure of two atmospheres being sufficient to carry on the functions.

Hyperpnœa is the term applied to the slightly increased amplitude and frequency of the respiratory movements, such as occur in gentle exercise, as the immediate result of any commencing defective oxygenation of the blood, or other cause which acts as a stimulus to the respiratory centre (see p. 136). When the stimulus is strong or continued, a further increase in the force and frequency of the respiratory movements takes place, and this condition is known as **dyspnœa.** The later stage of dyspnœa is characterised by the respiratory movements becoming 'convulsive' in their activity, and this finale to dyspnœa marks the onset of true asphyxia.

If the air supply be entirely cut off, asphyxia and death rapidly ensue. **Asphyxia** has been divided into three stages. In the first the attempts at breathing are laboured and painful, deep and frequent, and all the respiratory muscles, including the supplemental ones, are brought into play. Convulsions occur, and the blood-pressure rises. In the second stage the inspiratory muscles are less active, the expiratory still powerful, and the convulsions cease. In the third stage the animal lies unconscious, occasional violent inspiratory gaspings occur, the mouth is open (even in the horse), the pupils dilated, the pulse barely perceptible or absent. During this stage the blood-pressure rapidly falls. Death occurs in from five to six minutes from the commencement of the first stage. Young animals are less easily asphyxiated than adults for the reason that their tissue respiration is much less. The length of time necessary to drown puppies and kittens is evidence of this, and they may recover even after prolonged immersion.

Excess of Oxygen.—It has been shown that oxygen above a certain pressure it very poisonous. From 3 to 5 atmospheres of oxygen, corresponding to 15 to 25 atmospheres of air, suffice to kill seeds, hinder the development of eggs, and produce convulsions in warm-blooded animals. In these latter cases the amount of extra oxygen in the blood is 10 volumes, so that there are 30 instead of 20 in every 100 volumes of blood. This extra oxygen is not carried in the red cells, but in solution by the plasma. All animals are instantly killed by a pressure of 50 atmospheres of oxygen. The toxic nature of oxygen at high tensions is unknown. By increasing the amount of oxygen above that contained in air, the blood cannot be made to take up much more oxygen than if the normal amount only were present. A pressure of 10 atmospheres only causes an increase of 3·4 per cent. absorbed, so that the blood contains 23·4 per cent. of oxygen instead of 20 per cent. The practical application of this fact in the treatment of certain diseases by the inhalation of oxygen is interesting. If we double the amount of oxygen in the air, less than 1 per cent. of the extra addition is absorbed. Either the small amount of extra oxygen thus absorbed must be very valuable, or we must find some other explanation of the undoubted advantage of oxygen inhalation in disease.

The physiology of the matter is, in effect, this : The air contains 20 per cent. of oxygen, which is more than enough for the needs of the body. Even the venous blood returns to the lungs with from 10 to 12 volumes of oxygen per cent. unused, while if the oxygen in the air be doubled, less than 1 per cent. of the extra is absorbed. It may, however, be that the excess of oxygen in the alveolar air of the lungs during oxygen inhalation enables the tissues to obtain their normal amount more easily.

Apnœa is the term applied to a condition in which no respiratory movements of any kind are made. It is in the main a laboratory product, though it may also be met with in surgical operations. Apnœa may be produced artificially by blowing air into and sucking it out of the lungs at a more rapid and forcible rate than the ordinary respiratory rhythm of the animal. Two conditions have now been acting, either of which separately will produce apnœa. In the first place there is a very free lung ventilation, and in consequence a change in the composition of the gases in the alveoli of the lungs, and so in the blood of the medulla. The partial pressure of the carbon dioxide in the blood will be lowered, and as a result of the natural stimulus of the respiratory centre being withdrawn, the centre will remain inactive. This is not due, as was at one time supposed, to an excess of oxygen in consequence of free lung ventilation, as it will occur when the lungs are distended with hydrogen.

If the lowered pressure of carbon dioxide in the blood is the source of the suspended breathing, the introduction of this gas into the blood should abolish the apnœic condition. This is found to be so. A blast of CO_2 cuts short apnœa in the rabbit, while a blast of air has no such effect.

Another form of apnœa results from stimulation of the inhibitory fibres of the vagus by the repeated distension of the lungs. This condition cannot be produced if the vagi be divided.

The real value of the experimental production of apnœa lies in the light which it throws on the normal respiratory process, and it is very remarkable that the normal rate of breathing suitable to the animal's immediate requirements should be regulated by the carbon dioxide circulating through the medulla.

There is a surgical condition known as *shock*, common after prolonged operations, especially abdominal. In such there is a diminished amount of carbon dioxide in the blood, and in consequence a dangerous fall in blood-pressure. To this state the term **acapnia** has been applied. It is believed to result from the stimulation of afferent nerves increasing the pulmonary ventilation, but the exact condition is not yet decided.

The Nervous Mechanism Governing Respiration.—A large number of nerves is connected with the production of respiratory movements. The facial dilates the nostrils, the vagus supplies the larynx, the phrenic the diaphragm, certain spinal nerves supply all the muscles of the trunk engaged in respiration, and besides these purely motor functions, there are an enormous number of sensory nerves connected with respiration. Such extensive ramifications require for the proper discharge of their functions a central co-ordinating mechanism, and this is known to exist in the medulla. The position of this centre has in certain animals been very accurately defined, though it is not represented histologically by any special group of cells. In general terms it may be spoken of as being situated close to the deep-seated origin of the vagus, and in front of the vasomotor centre. The fibres which pass from it down the cord end in motor nuclei in the grey matter of different levels, corresponding to the outflow of the nerves connected with the muscles of respiration. There is also evidence of decussation of the fibres, or at any rate a connection between those on the right and left side of the cord, as we shall see presently in dealing with the phrenic.

The respiratory centre consists of two halves, each of which is capable of working independently. By some it has also been considered to consist of two parts—an expiratory and inspiratory. There is no definite indication of the former, but the latter is well marked ; and of the two acts the inspiratory is the most important, for, as we have already seen, expiration may, under some circumstances, be a purely passive act. Nevertheless, there are special expiratory functions of central origin, such as the act of straining, as in parturition, micturition, defæcation, and coughing—events which are certainly not of a passive character, and might be considered to originate in a special expiratory centre.

It is known that, besides the motor nerves previously described as being connected with the process of respiration, the respiratory centre is connected extensively with sensory nerves—probably every sensory nerve in the body, for the centre may be readily stimulated through any sensory branch. Further, the cortex of the brain is connected with the respiratory centre, for the animal may at will increase or withhold its respiration; while psychical events produce their effects through some such channel, as may be witnessed in the increased respiration of nervous apprehension. A perfectly orderly sequence of events occurs in normal respiration, beginning at the nostrils and ending at the flank, the entire smoothness and regularity of which is dependent on the nervous connections of the respiratory centre with the outside.

The centre is automatic—viz., it is within itself that the discharges are generated which issue forth as respiratory impulses; indeed, it is as automatic in its working as the heart, for if every nervous connection leading to it be divided, the centre continues notwithstanding to act rhythmically. If the chief path through which these impulses gain the exterior be cut—as, for instance, by dividing the spinal cord behind the medulla—death from paralysis of respiration at once ensues. Such a section does not affect the facial muscles of respiration, and an animal that has ceased to breathe and is virtually dead may still continue to make powerful inspiratory facial gasps, the nerves supplying these muscles being derived from a point anterior to the section.

The nature of the impulses which issue from the respiratory centre depends upon the character of the impulses received from without, which stimulate their production reflexly. Thus the breathing may be hastened or slowed down, quickened in rhythm and decreased in depth, or both rhythm and depth increased. From the cortex of the brain impulses may be transmitted, voluntarily increasing the respirations, as in sniffing, or withholding them entirely, as when the head is under water. Through the medium of the nasal branch of the fifth pair of nerves impulses may be transmitted from the nostrils inhibiting inspiration; from the skin impulses of two kinds are received—viz., those increasing and diminishing respiration. It has even been supposed that different nerve fibres are concerned in the transmission of stimulating or inhibiting impulses to the respiratory centre, though not exclusive channels for respiratory purposes. From the larynx through the superior laryngeal nerves impulses inhibiting inspiration and stimulating expiration are transmitted, and the same through the sensory fibres of the glosso-pharyngeal, which inhibits respiration at the moment of swallowing. In the diagram (Fig. 50) the chief nervous connections of the respiratory centre are shown; the sign denotes whether they convey impulses which stimulate or inhibit the respiratory centre.

The Influence of the Vagus on Respiration.—The vagus is the most important afferent channel by which the lungs are brought into connection with the medulla; the sensory fibres cover the area from the glottis to the alveoli of the lungs. If impulses from the lungs to the medulla are cut off by dividing the vagi, the respirations become slower and deeper (Fig. 51, C); in the horse they have been known to fall to five per minute; the inspirations particularly are deep and prolonged. If one vagus only be cut, the effect just described may not occur, or only be of a partial character. From this it is evident there are impulses passing up the vagus from the lungs to the medulla which maintain the normal respiratory rhythm, and these are permanently lost by section of the nerves. If the end of the divided vagus which is in connection with the brain be stimulated below the origin of the superior laryngeal nerve, there is arrest of respiration if the stimulation be strong, but with moderate stimulation it is quickened (Fig. 51, B). The strength of the stimulating current

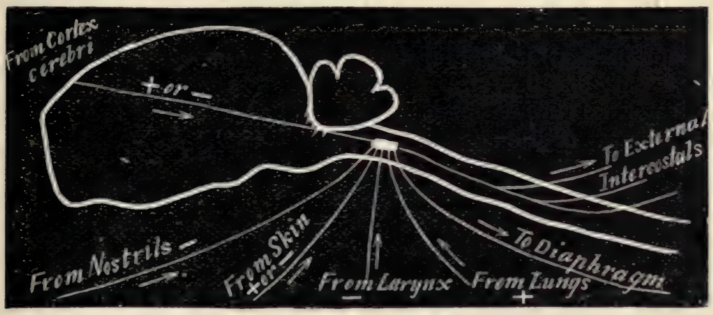

FIG. 50.—DIAGRAM TO ILLUSTRATE THE CHIEF NERVOUS CONNECTIONS OF THE RESPIRATORY CENTRE (AFTER WALLER).

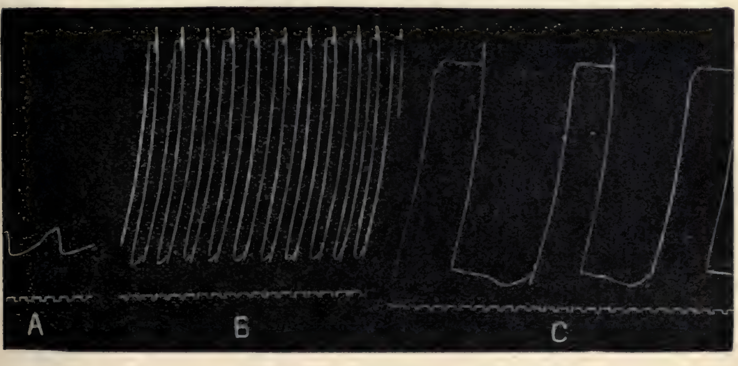

FIG. 51.—RESPIRATORY TRACINGS: DOG (STEWART).

A, Normal; B, effect of stimulation of the central end of vagus; C, effect of section of both vagi. Time tracing, seconds.

and the condition of the centre at the time of the experiment appear to be important factors in determining the exact results which will follow. But the interpretation of the results of these experiments is to show that there are two kinds of fibres in the vagus conveying impulses from the lungs to the medulla, and affecting it in opposite ways: (1) Fibres carrying impulses which cause inspiration and inhibit expiration; and (2) fibres conveying impulses which inhibit inspiration, and so cause expiration. These sets of fibres are in alternate activity, and the cause of their normal stimulation is believed to be the alternate distension and collapse of the air vesicles. If, for example, air be pumped into the lungs, expiration is excited, and if it be sucked out, inspiration follows; from which it is argued that an inspiration, by distending the air vesicles, excites expiration, and the contraction of the air vesicles on expiration excites inspiration. It can be shown experimentally that electrical changes in the divided vagus indicate a marked current throughout each inspiration, and another of a different character during expiration. If, however, the respiratory centre be regarded as primarily automatic, the inspiratory fibres found in the vagus may be looked upon as increasing the rate of respiration, the expiratory as inhibiting or controlling inspiration, and thus producing expiration. If this view be adopted, the act of inspiration proceeds from an automatic centre, which requires no other stimulus than that which is generated within itself, while expiration proceeds from the stimulation caused by distension of the air vesicles.

The nature of the internal stimulus which provokes the respiratory centre has for some time been the subject of controversy. All were agreed that it lay in the blood gases, but whether this was to be attributed to richness in carbon dioxide or poverty in oxygen could not for some time be decided. It is now pretty generally admitted that the richness in carbon dioxide is a more potent stimulant than poverty in oxygen, and Haldane's researches mentioned at p. 120 show the extraordinary delicacy of the respiratory centre's response to minute increases in carbon dioxide, a 0·2 per cent. increase leading to an increased pulmonary ventilation of 100 per cent.

During muscular work, especially that of a severe nature, there may be such substances as lactic acid in the circulating blood, which also act as a stimulant to the respiratory centre.

Respirations are increased in frequency as the result of sensory stimulation—such, for instance, as occurs in painful operations; sensory stimulation of the abdominal wall may be employed as a means of starting an inspiration in chloroform-poisoning.

Animals which do not sweat pant after work in order to get rid of the surplus heat by warming a larger volume of air. This question will be considered again under Animal Heat, but the possible mechanism involved may here be glanced at. It is conceivable that the congested condition of the skin may send impulses to the respiratory centre, but this will not account for the panting of animals in 'show condition.' Here there is presumably no increase in the carbon dioxide in their alveoli, and the stimulation to increased respiratory activity would appear to be obtained reflexly from the skin, though the increased temperature of the circulating blood in the medulla may account for it, as appears to be the case in fever.

Influence of the Phrenic Nerves on Respiration.—The phrenic is essentially an inspiratory nerve. We have referred to the cutting off of the respiratory centre by dividing the cord above the phrenic. If the cord be divided below the point of exit of the phrenics, the channel between the respiratory centre and lungs via the spinal cord is not interfered with, but the resulting paralysis of the abdominal and intercostal muscles necessitates that the action of the diaphragm should be more powerful. If one phrenic nerve be divided, half the diaphragm is paralysed; if both be divided, the whole diaphragm is paralysed, and in most animals causes death. In the horse division of the phrenic nerves is not fatal; it leads to difficulty in breathing, increased heart action, and the collection of fæces in the rectum; but in about twenty-four hours these symptoms pass away, and if the animal be worked, no appreciable difficulty in breathing is subsequently observed.

We are not prepared to offer any explanation of this remarkable exception to experimental division of both phrenic nerves. Sometimes the fact may be demonstrated in surgical practice, for though as a rule in the horse fracture of either of the four upper cervical vertebræ—viz., above the origin of the phrenic nerves—is immediately fatal, yet there are many exceptions to the rule, and death may be delayed for some time.

The phrenic nuclei in the cord are connected by crossed fibres, so that, if the cord be half cut through above the nuclei, both sides of the diaphragm are still able to contract, the explanation being that the impulses cut off from one half of the diaphragm are transmitted through the crossed channel.

Division of Seventh Pair.—Colin has shown that if the seventh pair of nerves be divided in the horse, and the animal worked, asphyxia results. This nerve dilates the nostrils; when divided, the paralysed flaccid nostrils are drawn inward at each inspiration, and so close the opening.

Cause of First Inspiration.—The cause of the first act of inspiration in the fœtus is that the placental circulation being cut off, the respiratory centre of the fœtus becomes stimulated through the increased venous character of the blood now circulating through it ; as a result of this, inspiration is automatically produced. But it is also assisted by reflex impulses carried from the surface of the skin due to handling and drying ; handling the skin of the fœtus while still *in utero* with the placental circulation intact may provoke respirations, and in all animals the very first act of the mother is to dry the fœtus and stimulate the skin by licking.

The Amount of Air Required.—Numerous respiration experiments have been made on all animals to determine the amount of air they require and the gases of respiration. The horse is, of all others, the one to which perhaps the greatest practical interest attaches in this respect, though a knowledge of it in connection with other animals is of value.

The lungs of a horse will contain about 42·5 litres (1½ cubic feet) of air at the end of a deep inspiration. During ordinary repose he draws into them 2,265 to 2,548 litres (between 80 and 90 cubic feet) of air in the hour, though considerable variation may be found even in the same animal.

An average inspiration in the horse during repose amounts to about 4·1 litres (250 cubic inches), and the amount of air which flows in and out during ordinary quiet respiration is known as the *tidal air*. Speaking roughly, it is only one-tenth of what the lungs can contain ; the remaining nine-tenths are made up of *complemental*, *reserve*, and *residual air*. The *complemental* air is that over and above the tidal which can be taken in by a forced inspiration, while the *reserve* is a somewhat similar amount which can be expelled by a forced expiration. The most powerful expiratory effort is unable to remove from the lungs all the air they contain, and this amount is known as the *residual* air.

The great variations which have been observed in the amount of air taken in by the same animals, under apparently identical conditions, cannot be adequately explained ; the slightest disturbing influence alters both the rhythm and depth of the respirations. Under the influence of work, the amount of air required is greater, and as a rule, the faster the pace the more air needed ; but many disturbing factors occur which render experiments on this subject very contradictory, and productive of the greatest variation. During severe work, such as a gallop, a horse is taking air into his lungs to the extent of 24,067 litres (850 cubic feet) per hour at least, and probably more ; the respirations, from being 9 to 10 per minute during repose, may now be anything between 70 and 100 per minute. The effect of taking in all this extra air is that the *pulmonary ventilation* is increased. It is calculated that in man a deep inspiration more than doubles the capacity of the alveoli by distending them. In such paces as the canter, trot, and walk, the amount of air used is correspondingly less ; immediately the pace slackens or the horse stops, the respirations at once fall, and the amount of air inspired becomes reduced. This is one of the great difficulties attending respiration experiments on horses under natural conditions.

In the following table is shown the mean amount of expired air obtained from horses performing actual work, and collected in the apparatus shown in Figs. 52 and 53:

	Air expired in Litres per Hour.	Air expired in Cubic Feet per Hour.
Repose - - -	2099·75	74·17
Walk - - -	3780·80	133·55
Trot - - -	8149·70	287·87
Canter - - -	11069·21	391·00
Gallop - - -	24038·02	849·10

A horse in a state of repose, according to Zuntz and Lehmann, produces 85 litres (3 cubic feet) of CO_2 per hour, and absorbs nearly 99 litres (3½ cubic feet) of oxygen ; the expired air is found to have lost 4 per cent. of its oxygen, and gained 3½ per cent. of CO_2. This is very much more than we found,* but it agrees pretty closely with the observations made on other animals and on man. It may be noted that even in animals which, from their small size or other causes, lend themselves to exactitude in experimentation, the most divergent results have been obtained, and the same thing is observed in man.

Muscular work has a profound influence over the respiratory exchange ; it increases the amount of oxygen absorbed and the proportion of carbon dioxide given off. The faster the pace the greater the amount of exchange which occurs, though experiment has failed to prove a definitely immediate relationship between the amount of oxygen absorbed and the amount of work produced.

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* 'The Chemistry of Respiration in the Horse during Rest and Work,' *Journal of Physiology*, vol. xi., 1890. It is now considered that samples of air are not sufficient to determine respiratory exchanges, the CO_2 has a tendency to accumulate in the tissues, and an apparatus which admits of prolonged observation is necessary, such as was employed by Zuntz and Lehmann.

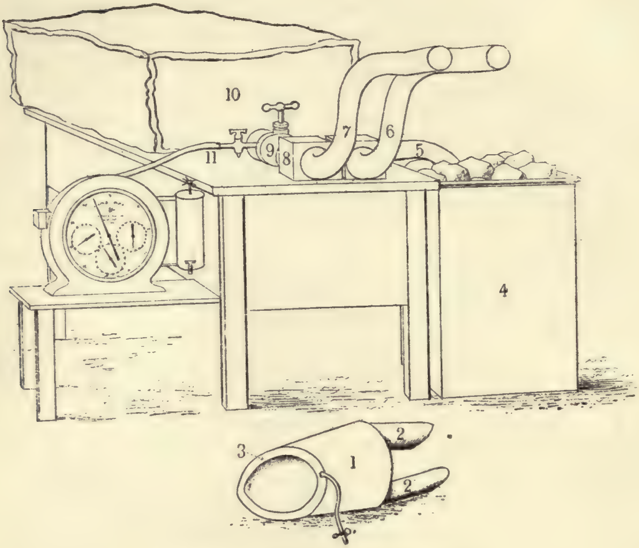

FIG. 52.—RESPIRATION APPARATUS.

1, The face mask ; 2, rubber connections with 6 and 7 ; 3, pneumatic collar to render mask air-tight above ; 7, inlet tube to bag ; 8, valve-box through which the expired air passes to 10, a rubber bag of 20 cubic feet capacity. After an experiment the air is pressed out of the bag, and, passing through 11, is measured in the meter. 4, A chamber containing a tray of coke saturated with caustic potash, through which the inspired air passes and is robbed of its CO_2 before entering 5.

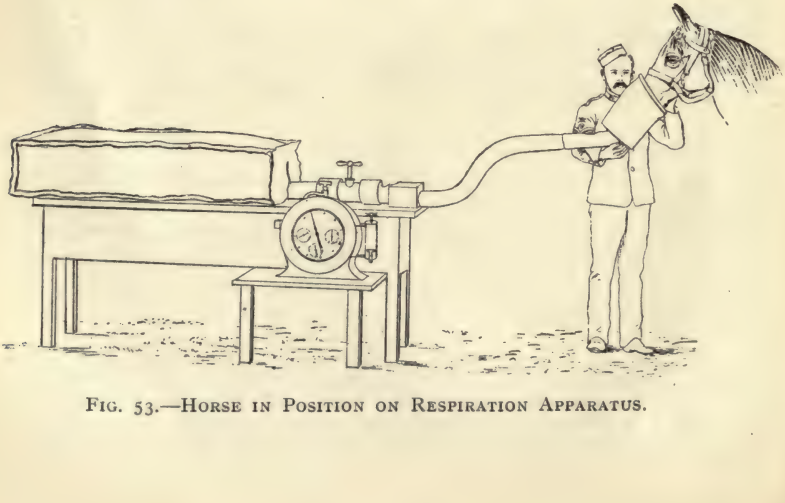

FIG. 53.—HORSE IN POSITION ON RESPIRATION APPARATUS.

The following table is taken from the experiments of Zuntz and Lehmann on horses:*

	Air expired per Hour.		Carbon Dioxide discharged per Hour.		Oxygen absorbed per Hour.		Respiratory Quotient.
	Litres.	Cubic Feet.	Litres.	Cubic Feet.	Litres.	Cubic Feet.	
Rest	2,640	93·2	88·68	3·13	96·06	3·39	0·92
Walk	10,620	375·1	260·52	9·20	285·96	10·10	0·90
Trot	19,980	705·7	450·96	15·90	485·58	17·15	0·93

The following table presented by Colin gives a general view of the respiratory changes in animals. It represents the mean of observations made many years ago by different authorities.

The column showing the respiratory changes per kilo of body weight illustrates the fact, to which attention will subsequently be drawn, that the changes among small animals are greater than among large ones, owing to their greater body surface relatively to their weight. The discharge of carbon dioxide by a mouse, for example, is relatively sixteen or seventeen times greater than that of an ox.

	Horse.	Cow.	Ass.	Pig.	Sheep.	Dog
Body Weight:						
Kilos - -	450	450	150	75	45	20
Pounds - -	990	990	330	165	99	44
Amount of air inspired in 24 hours:						
Litres - -	95,591	78,800	31,495	34,444	20,400	8,441
Cubic feet -	3376	2783	1112	1216	720	298
Grammes of oxygen consumed per kilo of body weight in 24 hours - -	13·272	11·040	13·577	29·698	29·314	28·392
Amount of oxygen consumed in 24 hours:						
Litres - -	4251·6	3456·0	1417·3	1550·0	918·0	397·86
Cubic feet -	150·0	122·0	50·0	54·7	32·4	14·0
Grammes of carbon dioxide produced per kilo of body weight in 24 hours	5·08	4·128	5·08	11·166	7·638	7·621
Amount of carbon dioxide produced in 24 hours:						
Litres - -	4285·55	3465·75	1427·52	1562·12	641·17	291·76
Cubic feet -	151·0	122·3	50·4	55·1	22·6	10·3

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* The work performed in these experiments was carried out on a platform revolving at different speeds, and the animal was thus kept in con-

The next table is given by Munk:

Animal.	Body Weight.		Oxygen absorbed Daily.		Carbon Dioxide given off Daily.	
	Kilos.	Pounds.	Litres.	Cubic Feet.	Litres.	Cubic Feet.
Horse	450	990	4270·0	150·800	4867	171·90
Ox -	600	1320	5565·0	196·500	5548	196·00
Sheep	70	154	605·2	21·377	580	20·48
Dog -	15	33	297·5	10·500	224	7·91

The Influence of Work on Respirations.—It is not clearly known why an increase in the number of respirations results from muscular work. During moderate work the increase of carbon dioxide in the alveoli of the lungs is sufficient, as we have seen, to increase the pulmonary ventilation; but with prolonged and especially severe work it is probable that there is formed in the muscle fibre some products of its metabolism, for example, lactic acid, which may, by circulating through the blood, either stimulate the respiratory centre, or render it still more sensitive to the percentage of carbon dioxide circulating through it.

Evidence that the panting respirations of work may be due to the presence of a chemical substance circulating in the blood is afforded by the experiment of dividing the spinal cord in the dog, and stimulating the muscles of the hind limbs. The animal, of course, is unconscious of any movement, but the respirations are increased as if it had been running for some distance. What the substance is that gives rise to this is not known. Lactic acid has been suggested, and dilute acids injected into the blood give rise to much the same condition. Hurried respirations may also be produced through the circulatory system. In an animal in training the breathlessness which it is one of the objects of training to get rid of, is due to the fact that more blood is brought to the lungs than can be disposed of. If the right heart pumps into the lungs more blood than the lungs can return to the left heart, breathlessness follows. The gallop by which an animal gets its 'wind' and 'staying' power, operates through the circulatory system. Fortunately, the vessels of the lungs are

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stant communication with the respiratory apparatus, from which samples of the expired air were taken for analysis. It has been shown that this latter is a necessary condition to insure accuracy. The writer's observations were carried out on horses which actually performed, under natural conditions, the various paces. These, however, are rejected as not sufficiently representing the respiratory changes occurring during work, owing to the samples of air being collected for too brief a period.

capable of considerable adjustment; they hold more blood during inspiration than expiration, and in this way may be regarded as a safety-valve to the heart. The important practical questions of work, 'condition,' and fatigue will be again referred to in the chapter dealing with the Muscular System.

Air vitiated by Respiration was at one time believed to be poisonous, either on account of its deficiency in oxygen, its increase in carbon dioxide, or to the organic matter mixed up with it. It is now generally admitted that the ill-effects of vitiated air are mainly due to the stagnation of the air and the warm and humid atmosphere, by which the respiratory exchange and body metabolism are affected. Even the number of bacteria in the air is no guide to purity; there may be fewer in expired air than in the same air before inspiration, in consequence of their being arrested in the lungs. Nevertheless, modern inquiry supports the principle contained in the old view, of the evil resulting from breathing atmosphere charged with CO_2. When the gas accumulates to the extent of 4 per cent., rapid breathing and general distress begin to be evident.

The amount of air required for effective ventilation is conveniently based on the amount of permissible impurity present, as judged by the proportion of carbon dioxide existing. Many observations show that when 0·02 per cent. of carbon dioxide is present, in addition to that in the air as a normal impurity—viz., 0·03 per cent.—the ventilation may be regarded as effective. On this basis, if the rate of CO_2 production by any given animal is known, it is easy to calculate the number of times the air of the building should be changed, in order to maintain it in a pure condition.

Respiratory Murmur.—An accurate acquaintance with the normal respiratory murmur is essential to the physician. The air sounds both of inspiration and expiration should be heard all over the chest, the inspiratory murmur being louder and better marked than the expiratory; in fact, in many perfectly healthy chests the expiratory murmur can scarcely be heard. The normal murmur, whether inspiratory or expiratory, is soft in character; there is no harshness. The sound is best represented by the noise made by the stream of air which issues from a pair of hand-bellows when gently blown.

The respiratory murmur, also known as the *vesicular murmur*, is caused by the friction of the air entering the alveoli. In those portions of the lung lying close to the bronchi and larger tubes there is, in addition to the vesicular murmur, a sound produced by the trachea and glottis. This is not distinct from the vesicular sound, but is added to it, the result being that the respiratory murmur over the tubes is louder than elsewhere. The expiratory sound is weaker and shorter than the inspiratory—that is to say, the sound is not continued to the end of expiration, but dies away before that is reached. The expiratory murmur immediately follows the inspiratory without a pause, but there is a marked pause between the end of one expiration and the beginning of the next inspiration.

The ordinary murmur is best heard where the chest wall is thin ; if the ribs be covered with fat or any great thickness of muscle, the sound may be entirely lost. It is also important to note that there are some chests perfectly healthy where, for no apparent reason, the respiratory murmur is obscure or even undetectable.

SECTION 2.

The Larynx.

The larynx serves a twofold purpose—viz., respiration and phonation; in animals the former holds the more important position, the voice-producing function being of a very subordinate character.

The larynx may be described as a cartilaginous box placed at the summit of the trachea, the opening into it being capable of increasing or decreasing in size, and so allowing a larger or smaller amount of air to enter the lungs. Within the larynx are two elastic cords arranged **V**-shaped, the function of which is connected solely with the production of sound (Fig. 54, 3). Both the respiratory and vocal functions require that the several parts of the larynx should move—viz., that the mouth of the organ should be widened or narrowed, or that the cords should be approximated, drawn apart, tightened, or slackened. These movements are brought about by certain groups of muscles, those which approximate the walls of the glottis being known as the adductors, whilst those which widen it are known as the abductors.

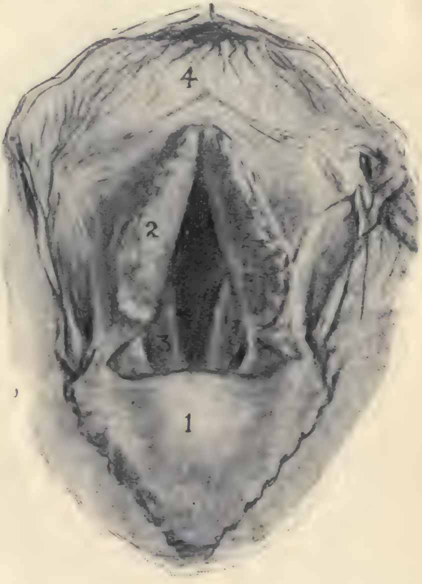

FIG. 54.—THE LARYNGEAL OPENING DURING ORDINARY RESPIRATION.

1, The epiglottis; 2, margin of arytenoids; 3, vocal cord; 4, pharynx laid open. The V-shaped slit is the glottis. Note how much wider the epiglottis is than the opening it has to cover.

The **Muscles of the Larynx** may therefore be divided into those of respiration and phonation. As the most important feature in respiration is the opening or dilating of the glottis, the term respiratory muscle might be confined to the dilator of the glottis, while the constrictors would represent the vocal muscles; but the constrictors are not entirely without a respiratory function, as, for example, in coughing, so that in the following table they are included under this head.

Respiratory Muscles.

Dilator or abductor,	*Crico-arytenoideus posticus.*
Constrictors or adductors of the glottis,	*Crico-arytenoideus lateralis, Arytenoideus, and Thyro-arytenoideus.*

These muscles are shown in Fig. 55.

The crico-arytenoideus lateralis and posticus are direct antagonists; the lateralis depresses the arytenoid cartilages and closes the entrance into the glottis, the posticus swings the arytenoids upwards and outwards and enlarges the glottis.

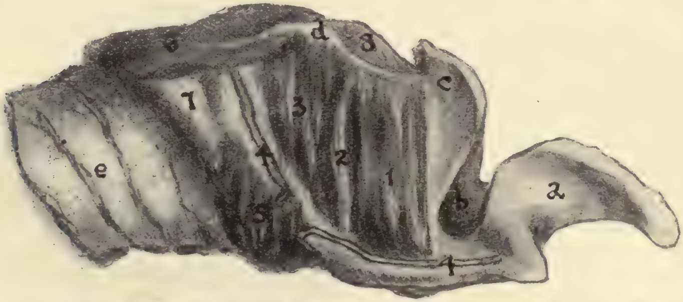

FIG. 55.—THE POSITION OF THE MUSCLES OF THE LARYNX IN THE HORSE.

a, Epiglottis; *b*, opening leading to the glottis; *c*, portion of the arytenoid cartilage; *d*, position of the joint formed between the cricoid and arytenoid cartilages; *e*, the trachea. The wing of the thyroid cartilage has been removed, so as to expose the constrictor muscles; 4, 4, represents its cut edge. 1 and 2, Thyro-arytenoideus; 1, anterior; 2, posterior fascicules. The space between these two muscles indicates the position of the ventricle of the larynx. 3, Crico-arytenoideus lateralis; 5, cricothyroid muscle, the bulk of which lies inside the thyroid cartilage, and cannot, therefore, be seen; 6, crico-arytenoideus posticus; 7, portion of cricoid cartilage. The shaded portion in front of the figure represents where it and the thyroid meet. 8, Arytenoideus muscle.

Phonatory Muscles.

Muscle which relaxes the vocal cords,	*Thyro-arytenoideus*, anterior and especially posterior fasciculus.
Muscle which renders the cords tense,	*Crico-thyroid.*
Muscles which bring the cords together,	The respiratory adductors.
Muscle which moves the cords apart,	The respiratory abductor.

The entrance to the larynx is formed by the two arytenoid cartilages, the epiglottis, and the aryepiglottic folds; beyond these is the glottis proper—viz., the **V**-shaped opening formed by the vocal cords. When the laryngeal opening dilates, the vocal cords pass towards the wall of the cavity and render the **V**-shaped space wider; when the larynx closes, the cords are approximated and the space rendered narrower (Figs. 54 and 56). During ordinary respiration there is very little if any alteration in the shape and size of the glottis; but during exertion every inspiratory movement is accompanied by an increase in size, every expiration by a decrease. At each expiration the vocal cords pass towards the centre line, and at each inspiration return to the wall of the larynx. The closure of the larynx, such as during the act of swallowing, is a powerful movement, and if the finger at this moment be introduced into the cavity and placed between the arytenoids, it experiences considerable pressure. The closure of the larynx is brought about by the depression and approximation of the arytenoid cartilages and the approximation of the vocal cords; in addition, during the act of swallowing, the base of the tongue presses the epiglottis over the arytenoids and renders the part both air- and water-tight.

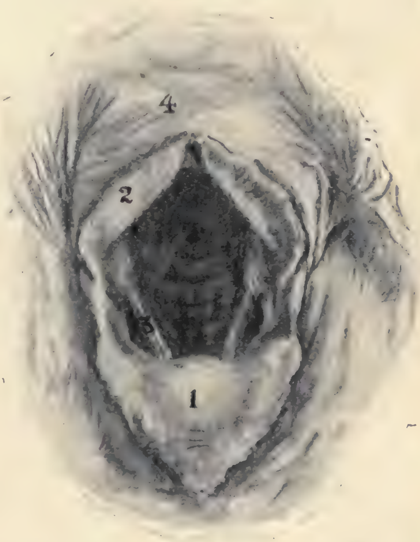

Fig. 56.—The Laryngeal Opening during Hurried Respiration, seen in a State of Dilatation.

1, Epiglottis; 2, margin of arytenoids; 3, vocal cord; 4, pharynx laid open. Note the size and shape of the glottal opening as compared with Fig. 54.

The **Epiglottis** is much larger than the opening it is intended to seal during a condition of laryngeal repose. It is carried backwards by the base of the tongue and pressed over the arytenoids; the larynx at the same moment advances, with its arytenoid cartilages closely approximated. After the act of swallowing, the tongue advances, the larynx recedes, and the epiglottis returns to its position by means of its elastic recoil. It is not essential to a food- or water-tight condition of the larynx that the epiglottis should exist ; it has been removed both by disease and experimentally, and its place is then taken by the base of the tongue. Nor is an arytenoid cartilage essential to safety in swallowing.

The **Nervous Mechanism of the Larynx** is peculiar. Sensation to the mucous lining membrane and motor power to the crico-thyroid muscle is supplied in the majority of animals by the superior laryngeal branch of the vagus, this nerve containing both sensory and motor fibres. In the horse the motor fibres running in the superior laryngeal are, it is said, derived from the first cervical nerve and not from the vagus. All the other muscles, both abductor and adductor, are supplied with motor power by the inferior or recurrent laryngeal branch of the vagus. It is strange that both abductor and adductor muscles should have the same source of nerve supply, and one naturally asks what it is which determines that only the opening or only the closing muscles shall act at any given moment ? The explanation of this fact lies in the law of ' reciprocal innervation,' demonstrated for the limb muscles by Sherrington, which will be considered later in the chapter on the Nervous System. Both dilator and constrictor fibres run in the recurrent laryngeal nerve, and are quite distinct ; in some animals the different bundles have been experimentally isolated and injured—injury to the dilator fibres producing abductor paralysis, and injury to the fibres going to the muscles which close the larynx, producing adductor paralysis.

If the recurrent laryngeal be cut and the peripheral end strongly stimulated, the glottis almost invariably is found to close ; in other words, only the adductor fibres appear to be acted upon. If a *weak* stimulation be applied, the glottis opens—viz., the abductor muscles are affected.

Another curious fact in the history of the recurrent nerves is furnished by pathology. In the disease of horses known as **' roaring,'** there is paralysis of the left abductor muscle of the larynx—viz., the crico-arytenoideus posticus, the wasting and fatty degeneration due to paralysis being very marked. It is not unusual to find the adductor muscles normal in appearance, or presenting very little sign of disease, and even if pale and wasted the degree of degeneration cannot be compared with that furnished by the abductor muscle. This is a difficult fact to explain ; one would think that as both abductor and adductor muscles receive the same nerve supply, equal wasting would occur in both groups. Again, it is observed when the recurrent has been divided experimentally that the abductor muscle loses its irritability long before the adductors, and the same fact may be observed in post-mortem stimulation of the nerves. If the recurrent laryngeal nerves be divided under ether, and the peripheral ends stimulated, adduction of the larynx is obtained; but if the ether narcosis be pushed to a dangerous extent and the nerves then stimulated the glottis dilates, that is, abduction follows. These and other observations have furnished a law which is of clinical significance—viz., that in *functional* disturbance of the larynx the adductor muscles are first affected, but that in changes accompanied by organic lesions the abductor muscles are the first to suffer.

When one recurrent laryngeal nerve is divided, the vocal cord on that side remains immovable and therefore cannot approach its fellow; the healthy cord endeavours to compensate for the weakness of its companion by passing beyond the middle line of the larynx in its attempt to come into contact with it.

The inspiratory distress occasioned in 'roaring' is not brought about, as has been described, by a paralysed vocal cord flapping about, for the elastic nature of the cord, and the fact that the only muscle never affected with paralysis is the one which helps to keep the vocal cord tense, negative this. The sound is produced by the paralysed left arytenoid cartilage being drawn into the glottis at each inspiration, and this is the explanation why the noise which accompanies the disease is always *inspiratory* and never expiratory.

Phonation.—Voice is produced by the approximation and vibration of the vocal cords, the *pitch* of the voice being produced by the tension of the cords, whilst the *quality* is due to the shape of the cords—viz., their thickness or thinness. The position of the resonant chambers such as the mouth, pharynx, posterior nares, and even nasal chambers also importantly affects the quality of the voice. It is obvious that the chief alterations in the larynx during phonation refer to the vocal cords; these are approximated by the adductor muscles, and separated by the abductor muscles, whilst they are relaxed by the thyro-arytenoideus and tightened by the crico-thyroid. The latter muscle has a peculiar action; it lowers the thyroid cartilage on the cricoid and swings the wing of the thyroid outwards, thus rendering the cords tense. These changes in the vocal cord produce changes in the shape of the **V**-shaped glottal opening; in a high note the glottis is reduced to a mere slit, in deeper notes the cords are separated. If air be forced through the larynx of a dead horse and the tension of the cords altered, a sound remarkably like a neigh may be produced. The ventricles of the larynx and cavities of the mouth, nose, pharynx, etc., act as resonators. Being filled with air, they effect the needful alterations in the quality of the voice, and assist in giving it its distinctive character; thus the false nostrils furnish the 'snort' of the frightened or 'fresh' horse, the nasal chambers the whinny and neigh of pleasure, the mouth and pharynx the neigh of impatience, loneliness, excitement, etc. We do not consider that the guttural pouches act as resonators, and Colin obtained no alteration in the character of the neigh by opening them.

The voice of each class of animal—horse, ass, ox, sheep, and pig—is so distinctive that we may recognise their presence without seeing them; yet though the larynx in all these animals differs more or less, the difference is not sufficient to offer any explanation as to why the sounds it emits are so entirely distinct. The voice of male and female animals differs in intensity. The wild neigh of the stallion is very different from the neigh of the mare, and the bellowing of the bull is distinct from the 'lowing' of the cow. The operation of castration has a remarkable effect on the voice, the neigh of the gelding resembling that of the mare.

In the horse the voice is used during sexual and ordinary excitement, also during fear or especially loneliness, during pain, anger, and as a mark of pleasure. It is not possible to convey in words the difference in the notes produced, but they are easy to recognise. The horse is essentially a sociable animal; when accustomed to be in the company of others he dislikes separation, and shows it by persistent neighing, which is perhaps more noticeable amongst army horses than any others. The neigh of pleasure is often spoken of as the 'whinny'; the word rather conveys an idea of the sound made. Sounds which can only be described as 'screams' are often evoked during 'horse-play' and temper, or by mares during œstrum. It is not a scream as we know it in the human subject, but no other word conveys an idea of its shrillness. If a horse cries from pain (which is very rare), as during a surgical operation, the cry is a muffled one and short; it is a groan rather than a cry.

In the cerebral cortex voice is represented in the præcrucial and neighbouring gyrus of the dog, and corresponding regions in other animals. Stimulation of this region leads to *bi-lateral* adduction of the cords, which suggests that both sides of the larynx are represented in each hemisphere. There is no region in the cortex of the dog which, on stimulation, leads to abduction of the cords, though such a region is found in the cat. It would appear that adduction of the cords is represented in the cortex, as the muscles producing it are especially associated with the production of voice, which is under the influence of the will. Respiration, on the other hand, is automatic, and the abductor muscles being essentially respiratory, their centre is found to exist in the medulla.

Neighing in the horse is produced by an expiration, partly through the nostrils and partly through the mouth; **braying** in the ass is both inspiratory and expiratory, nostrils and mouth each taking a share in it. The ventricles of the larynx are large in the horse and relatively still larger in the ass and mule ; they act as resonators and allow of free vibration of the vocal cords. According to Chauveau both ass and mule have the subepiglottic sinus provided with a thin membrane capable of vibrating. In the ox, sheep, and goat, the larynx is very simple, there are only rudimentary vocal cords and no ventricles. The **bellowing** of the ox and **bleating** of the sheep are expiratory efforts through the mouth. The dog and cat have a larynx something like that of the horse, but the ventricles are shallow ; the voice is produced almost entirely through the mouth, though both growling and purring may occur through the nostrils.

Yawning is a deep, slow inspiration followed by a short expiration ; the air, even in the horse, is taken in by the mouth, which is widely opened and the jaws crossed.

Sneezing and **Coughing** are expiratory efforts. The former occurs solely through the nose, and, excepting in the dog and cat, is unaccompanied by the peculiar sound attending this act in the human subject. If snuff be introduced into the nostrils of the horse, a peculiar though well-known vibration of the nostrils occurs as if the animal were blowing its nose, and this is, in fact, what it accomplishes. It is an entirely nasal sound ; the mouth takes no share in the act. Coughing occurs through the mouth, the long palate in the horse being raised for the purpose. Before coughing can occur the lungs must be filled with air and the glottis closed ; a forcible expiration follows, the glottis opens, and the air is expelled through the mouth.

Hiccough is due to a sudden contraction of the diaphragm. While the air is rushing into the lungs the glottis closes, and the incoming air, striking the closed glottis, produces the sound. The condition known as spasm of the diaphragm in the horse is very different from a human hiccough, and ~~has been~~ referred to more fully on p. 152.

Pathological.

Pneumonia and Pleurisy in the horse are very common in early life, and attended by a high mortality. The lungs and pleura, separately or combined, may suffer a degree of inflammation varying from small localised trouble to general and extensive inflammation of the pleura and lungs. The whole of the lung tissue is never affected ; even in the most severe cases of pneumonia there is some breathing area available : the upper portion of both lungs generally escapes. Effusion of fluid into the cavity of the thorax is a common sequel to pleurisy in the horse.

Both the above pathological conditions and their progress are diagnosed by auscultation and percussion : there are many departures from the normal respiratory murmur, all of which have their significance.

Apoplexy of the Lungs arises as the result of overwork, especially in hot weather; but it may also occur in the winter. Horses ridden to death in the hunting field, in the name of 'sport,' die as a rule from pulmonary apoplexy; the lungs cannot get rid of their abnormal burden of blood to the left heart.

Bronchitis is probably rarely a disease distinct from pneumonia.

'Broken Wind' is one of the most interesting of the various chest diseases of the horse; it is a condition peculiar to this animal, liable to occur suddenly, and frequently traced to errors in dieting. To state the case shortly, *the lungs lose their power of elastic recoil*, and do not collapse even after death; the respirations are greatly increased, the expiratory effort being powerful, characteristically irregular, and prolonged. A chronic typical cough becomes established, and the animal unfit for anything but slow work. On post-mortem examination the lungs are found to fill the chest entirely; they cannot collapse, for all elastic recoil has left them. One of the fundamental errors in veterinary pathology is to attribute this condition to emphysema or asthma.

Roaring is a nervous affection, to which sufficient allusion is made in the section dealing with the larynx. One point may be established in consequence of the frequency with which the larynx is now surgically dealt with, and that is, an injury to a cartilage of the larynx is always followed by thickening and ossification, with consequent reduction in the lumen of the larynx.

Spasm of the Diaphragm is another respiratory affection due to disordered nervous supply. The sound emitted is quite unlike that in the human; it appears to come from within the chest or abdomen, and is represented by a dull 'thud' like a magnified heart-beat, which, in its frequency and regularity, it closely resembles, and for which it may easily be mistaken.

Rupture of the Diaphragm is a common lesion frequently due to disorders of the digestive canal, the gas generated in the intestine being sufficient to burst the diaphragm. Falls are by no means an uncommon cause; for example, an animal falls on to its head, and the abdominal viscera are propelled against the diaphragm. The diaphragm rarely gives way below, almost always above, and in the tendinous substance rather than the muscular. This point is of physiological interest.

Catarrh.—As the horse can only breathe through the nostrils; obstruction of these passages from catarrh render the animal unfit for work, even when no other symptoms of importance are present. In the facial sinuses collections of pus are frequent and troublesome.

Laryngitis is frequently the result of strangles infection, rarely of ordinary cold. In the former condition local œdema and dyspnœa are not infrequent, and arise suddenly.

In the ox pneumonia is rare, with the exception of the specially highly infectious type, constituting one of the animal plagues. Practically none of the other diseases mentioned above as affecting the horse are found in any ruminant.

The number and character of the respirations is not only a trustworthy guide during the onset and progress of disease, but their character may be absolutely diagnostic. Broken wind and hydrothorax may be determined by a glance at the flanks; stertorous breathing suggests cerebral compression; while any noise accompanying the inspiratory act in the horse is suggestive of commencing œdema of the pharynx or larynx.

CHAPTER V

DIGESTION

SECTION I.

Digestion in the Mouth.

Prehension of Food.—The methods by which animals convey food to the mouth differ according to the species. In the horse the lips play an important part, for which purpose they are thick, mobile, remarkably strong, and endowed with acute sensation; in the ox they serve a subordinate function, being rigid and wanting in mobility; in the sheep the upper lip is cleft in such a manner as to divide it completely into two parts, each possessing independent movement; in the pig the lower lip is pointed and the upper one insignificant.

In manger feeding the horse collects the food with the lips, but in grazing cuts off the grass with the incisor teeth, drawing the lips back in order that they may bite closer to the ground. In the ox the tongue is protruded and curled around the grass, which is thus drawn into the mouth and taken off between the incisor teeth and the dental pad. In the sheep the divided upper lip allows of the incisors and dental pad biting close to the ground, so that animals of the sheep and goat class can live on land where others such as the horse and ox would starve. In whatever way the food is cut off, it is carried back by the movements of the tongue to the molar teeth, there to undergo a more or less complete grinding.

In the ox and sheep the incisor teeth move freely in their sockets; the object of this is to prevent injury to the dental pad, for which purpose also they are placed very obliquely in the jaw. In the horse the incisor teeth in early life are very upright, but become oblique with age. The molars in all herbivora are compound teeth; in the horse they are very large, especially those in the upper jaw. Being composed of materials of different degrees of hardness they wear with a rough surface, which is very essential to the grinding and crushing they have to inflict on grasses and grain. The teeth in herbivora, both incisors and molars, are constantly, though slowly, being pushed out of the sockets which hold them ; in this way wear and tear is compensated for, whilst the fang of the tooth becomes correspondingly reduced in length. It is owing to this fact that the incisor teeth alter in shape and direction, and so enable the age to be determined. The tables of the molar teeth are not flat but oblique ; this is especially well seen in the horse where the cutting surface is chisel-shaped, the upper teeth being longest on the outside, while those of the lower row are longest on the inside (see Fig. 57). This arrangement produces sharp teeth, which are a constant source of trouble and loss of condition in horses.

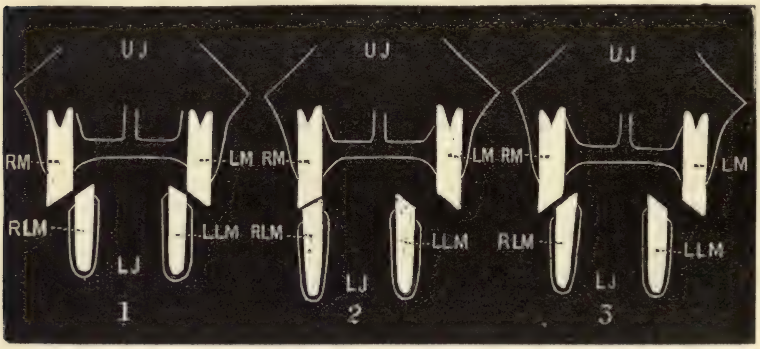

Fig. 57.—Schematic Transverse Section of the Upper and Lower Jaws of the Horse between the Third and Fourth Molars, showing the Position of the Tables of the Teeth during Rest and Mastication.

UJ, Upper jaw ; LJ, lower jaw ; RM, right molar ; LM, left molar ; RLM, right lower molar ; LLM, left lower molar. 1, The position of the teeth during rest, the outside edge of the lower row in apposition with the inside edge of the upper. 2, The jaws fully crossed masticating from left to right ; the tables of both upper and lower molars now rest on each other. 3, The position halfway through the act of mastication ; the outer half of the lower teeth wearing against the inner half of the upper.

The movements of the tongue are important. In the ox and dog they are very extensive, the former animal having no difficulty in protruding the tongue and even introducing the tip into the nostrils. It is not a very common habit with horses to protrude the tongue except when yawning, but they have considerable power in withdrawing it in the mouth. A great difference exists between the tongue of the horse and that of the ox ; the former is flabby, broad and flat at the end, constricted opposite the frenum, and swelling out at the apex ; it is comparatively smooth on its surface. The tongue of the ox narrows from base to apex, the latter being pointed ; it is very rough, which prevents it from losing its hold on the food, protects it from such injury as might be inflicted by coarse grasses, and is also of value to the animal in cleaning its body. The tongue is supplied with motor power by the hypoglossal nerve and with sensation by the lingual branch of the fifth, which supplies the anterior two-thirds of the mucous membrane, the posterior third being supplied by the lingual branch of the glosso-pharyngeal; the same nerve also supplies the sense of taste to this part of the organ, while taste for the anterior two-thirds is supplied by the chorda tympani of the seventh pair. Division of the hypoglossal nerve in the ruminant prevents the animal from grazing, the dog from lapping, and in all animals the tongue suffers injury by being unable to avoid the incisor teeth.

The inside of the mouth of the ox is covered with long papillæ, which point backwards; these would appear to be of use in preventing the food from falling out of the mouth. In the horse no such papillæ exist, in fact the lining membrane of this part is remarkably smooth. The majority of animals have grooves in the palate; they are well marked in the horse, ox, sheep, and even in the dog. Their function is probably connected with assisting the tongue to pass the food back in the mouth.

Drinking is performed by the animal drawing the tongue backwards and thus using it as the piston of a suction-pump; this action produces a vacuum in the front of the mouth, as the result of which the cheeks are drawn inwards, the lips at the same time being closed all round, excepting a small space in front which is placed under water. Such is the method in both horse and ox; in the former animal the head is extended while drinking, the ears are drawn forward at each swallow, and during the interval fall back. The cause of this motion is not clear, but is probably due to the movement of air in the guttural pouches. A thirsty horse will swallow from 150 to 250 grammes (5 to 8 ounces) of fluid at each gulp. Lapping in the dog is performed by curling the tongue in such a way as to convert it into a spoon. Sucking, like drinking, is produced by the animal creating a vacuum in the mouth by closing the lips, decreasing the size of the tongue in front and increasing it behind, the dorsum being applied to the roof of the mouth. The foal places the tongue beneath the nipple and curls it in from each side; by this means he protects it from the lower incisors and gets a better hold.

Mastication.

Mastication is performed between the molar teeth; the movements which the jaws undergo, to admit of this being carried out, depend upon the class of animal. In the dog they are very simple, being only a depression and elevation of the jaw; this motion means a simple temporo-maxillary articulation, and such is met with in this animal. In the horse and ox the movement is not only up and down, but lateral, and some say even from front to rear. This necessitates a complex joint capable of affording a considerable amount of play, and this is provided by a disc of cartilage being placed between the articulation, which accommodates itself to the varying movements of the joint in the horse, ox, and sheep, and also saves the part from jar. In herbivora, therefore, we find the cartilage extensively developed, whilst in carnivora it is small and simple. The character of the movement occurring in the temporo-maxillary articulation of herbivora during mastication is as follows: During rotatory movement, or lateral displacement, one of the articulating heads remains as a fixed point simply turning on its centre, whilst its fellow describes an arc; this is why the movement can only occur on one side at a time (Colin). During mastication the contents of the orbital fossæ are observed in the horse to be alternately ascending and descending. This movement is due to the coronoid process of the lower jaw, the fossa being pushed up as the process comes forward and depressed as it recedes. The muscles which bring about this important lateral movement of the jaws, which in the ox, owing to the freedom of the articulation, may be termed rotatory, are the two pterygoids, especially the internal. The herbivora can only masticate on one side at a time; when tired on one side the process is reversed, and the opposite molars take on the crushing. It is surprising the length of time an animal will carry on mastication on one side; even as long as an hour has been observed in the horse by Colin. This observer noticed that in the ox the first stroke of the molars is in the opposite direction to the regular action which follows; thus, if masticating from right to left the first stroke is made from left to right. It is important to note that in those animals where a single-sided lateral or rotatory movement in mastication is necessary, the upper jaw is always wider than the lower; this we can understand, for if both were the same width the molar teeth would not meet each other when the jaws were crossed for lateral mastication. This extra width of the upper over the lower jaw, in conjunction with the peculiarity of mastication, explains why the molar teeth of the horse and other herbivora wear with sharp chisel edges (see Fig. 57).

Mastication in the horse is a slow process, though 'greedy' feeders are not unknown. The grinding is very thoroughly performed. The resulting semi-liquid mass weighs from 50 to 100 grammes (1 to 2 ounces), takes about half a minute to produce, and necessitates as a rule about 40 crushings between the molars before being fit for swallowing. This data gives some notion of the amount of work performed by the masseter muscles in eating, say, 2 kilogrammes (4·4 pounds) of hay. Colin, whose results are given above, shows that it took 5 horses, the following time to eat 2 kilogrammes of hay: 1 hour, 1¼ hours, 1 hour 12 minutes, 1½ hours, 1¾ hours, the latter being a very small horse, while the second animal in the series was a big one. The average rate of crushing is 70 to 80 per minute, while the amount of work performed by the jaws working at 420 to 480 times an hour constitutes a distinct source of daily loss. Colin shows that when the animal is very hungry he will prepare and swallow 30 balls in 15 minutes, but as he gets satisfied he does not make more than 10 or 12 swallows in the same time. If the flow of saliva be reduced in amount, the length of time occupied by mastication is naturally increased.

According to the writer's observation, it takes a horse 15 to 20 minutes to eat 1 pound of hay, and 5 to 10 minutes to eat 1 pound of corn.

With the ox the first mastication is imperfectly performed, and is three times quicker than in the horse. When, however, the material is brought back for remastication, the process is slow. In the dog mastication is imperfectly performed; after a few hasty snaps of the jaw the material is swallowed.

Opening the mouth is equivalent to depressing the lower jaw, for the upper takes no share in the process. The muscles which open the mouth are comparatively small, for very little effort is required; the *sterno-* and *stylo-maxillaris* and *digastricus* perform this function. On the other hand, the closing of the jaws in mastication is a difficult task, and for this purpose very powerful muscles exist, they are the *masseters*, *temporals*, and *pterygoids*. In the dog the temporal muscles are considerably developed, whilst in herbivora the masseters are the largest.

The nerves employed in mastication are the sensory fibres of the fifth which convey to the brain the impulses resulting from the presence of food in the mouth, while the motor fibres of the same nerve supply the needful stimulus to all the muscles of mastication excepting the *digastricus*, which receives its motor supply from the seventh pair.

Deglutition.

The process of swallowing is usually described as occurring in three stages. The first stage practically comprises carrying the food back to the base of the tongue and pressing it against the soft palate; it is a simple process and readily understood. In the second stage the act is complex, for the bolus or fluid has to cross the air passage, and must be prevented from falling into the nasal chambers, or finding its way down the trachea. To accomplish this the soft palate is raised and so closes the nasal chambers, the tongue at the same time being carried backwards, while the larynx and pharynx are advanced. This movement causes the base of the tongue to press on the epiglottis and close the larynx, which is further secured by the arytenoid cartilages and vocal cords coming close together. The bolus, liberally coated with mucus from the large mucous crypts in this locality, or fluid, can now safely pass towards the pharynx, being grasped by the pharyngeal muscles and pressed into the œsophagus. In the third act of swallowing the food is carried down the œsophagus by a continuous wave of contraction, which starts at the pharynx and ends at the stomach. Chauveau points out that, owing to its extreme length, the soft palate of the horse passes completely into the pharynx during the second act of deglutition. The length of the soft palate in this animal prevents food or water being returned by the mouth when once they have entered the pharynx, so that in vomiting, or in cases of sore throat, the food, water, or other material is returned by the nostrils.

It is now considered that in some animals the constrictor muscles of the pharynx take less share in the process of swallowing than was at one time supposed, and that the sharp contraction of the mylo-hyoid muscles of the tongue, together with a backward movement of the organ, exerts pressure on the bolus, and shoots the latter through the pharynx into the œsophagus. From the time the mylo-hyoids act until the entrance of the food into the œsophagus, only a second elapses. We are not inclined to think these observations can at present be applied to swallowing in the horse. If the hand is placed in the pharynx there is no suggestion of any such shooting movement, and material, such as a bolus, placed far back on the tongue, is frequently very deliberate in entering the œsophagus.

The action of the epiglottis in the closure of the glottis has been much discussed. In the horse it is forced over the opening by the base of the tongue and the advancing larynx; but the epiglottis is not essential to swallowing, for an animal can swallow when it has been removed, and even when one of the arytenoid cartilages has been excised. With a finger in the larynx it can easily be demonstrated that the part closes tightly and forcibly during the second stage of swallowing, the vocal cords and arytenoids being brought so close together that the glottis is perfectly air-tight. It has been pointed out that animals usually swallow with a flexed neck, as in this position the epiglottis is behind the soft palate, and in the most favourable position to be applied over the glottis; it has also been shown that when the head is extended the epiglottis is in the mouth—viz., anterior to the soft palate. We have found it in this position in the horse, and judging from the fact that in a state of nature the horse and ox swallow with an extended and not with a flexed neck, it is probable that in feeding off the ground the epiglottis is anterior to the soft palate. During the third stage of deglutition the bolus can be seen slowly travelling down the channel of the neck; if liquid, however, be passing, the movement is very rapid, for as many as sixty swallows may be made in a minute. Both in eating and drinking the third act of deglutition can occur against gravity; this is because it is a muscular act. The whole process of deglutition is considerably assisted by the salivary secretion. When this has been experimentally diverted, swallowing only occurs with difficulty and very slowly.

It is now generally recognised by physiologists that the passage of material along the œsophagus depends upon its consistency: if fluid, it is shot along from end to end by the one act of swallowing, whereas, if it is solid material, it passes along by the process of peristalsis. The wave begins behind the pharynx, the circular muscle contracts, and its action is helped by the immediately preceding contraction of the longitudinal muscle, which thereby shortens, and so tends to dilate the tube for the reception of the bolus. In man liquids may be shot into the stomach in 0·1 second, but solid material is believed to occupy 6 seconds for the peristaltic wave to reach the stomach. Judging from the rate of progress of a bolus along the cervical portion of the œsophagus of the horse, 3 or 4 seconds might be occupied from pharynx to stomach; and taking into consideration the far greater length of the œsophagus as compared in man, it would appear that the rate of peristalsis is quicker in man. In rumination, as we shall see, the rate is very quick, 1½ seconds from pharynx to stomach.

The œsophagus of the horse is found to differ considerably from that of most other animals. It is composed for the greater part of its length of red striated muscle, while at and near its termination the previously thin muscular coat becomes very thick and rigid, and the red gives way to pale, non-striped muscle; further, the lumen of the tube becomes very narrow. The thick terminal end of the œsophagus of the horse is always closely contracted, so that if cut through close to the stomach no material can escape; this is one explanation why horses vomit with such difficulty. In the ox, sheep, and dog, the tube is composed of red muscle throughout; it terminates in a dilated end at the stomach, and, owing to its thin, distensible walls, even bulky material can pass along it; what the ox and dog can swallow with ease would certainly 'choke' the horse.

It is now believed that in man liquid or liquid foods are held up at the cardiac end of the œsophagus and slowly pass into the stomach, the opening into which is controlled by a sphincter. We have never observed anything in the horse which would lead us to assume a similar action. The cardiac sphincter in this animal is very powerful, and extends some inches up the œsophagus; food may sometimes be found in it which has failed to obtain an entry to the stomach, but it is always trifling in amount.

The first stage of deglutition is voluntary, but the remaining processes are quite involuntary, and are brought about by the stimulation of a centre in the medulla known as the swallowing centre. By means of ingoing or afferent nerves supplied by branches of the fifth and the superior laryngeal, the centre is made acquainted with the fact that food is present in the fauces. A reflex act is now set up in the centre, and an impulse conveyed to the muscles of the part by outgoing or efferent nerves, furnished by the pharyngeal plexus (composed of the vagus and glossopharyngeal) to the constrictor muscles of the pharynx, by the hypoglossal to the tongue, and by the recurrent laryngeal to the muscles which close the glottis. The glosso-pharyngeal is the inhibitory nerve of deglutition; if the central end be stimulated it is impossible to produce the act of swallowing. Further, it is the nerve which immediately inhibits respiration during swallowing, no matter at what phase of the act—viz., inspiration or expiration—the stimulus is applied. Swallowing may be induced without the presence of food in the fauces; touching the rim of the glottis will produce it; so also will pouring a fine jet of fluid into the trachea, or even touching the interior of the trachea as far down as the bronchi.

Stimulation of the mucous membrane of the pharynx excites reflex movements of the œsophagus, but stimulation of the mucous membrane of the œsophagus itself is ineffective in this respect.

The swallowing centre also presides over the œsophagus, and the peristaltic wave from the pharynx to the stomach is produced by impulses sent out from this centre through the vagus. This wave is, therefore, not due to the nerve handing on a contraction by direct conduction from one layer of the muscular wall of the œsophagus to the next. Hence, when once started, it is not arrested either by ligaturing or dividing the œsophagus, though section of the œsophageal nerves prevents it. The contraction wave which sweeps along the œsophagus is not interfered with even by excising a portion of the tube; the wave, having reached the point from which the upper segment has been cut out, appears in due course at the point from which the lower end was removed.

It is not uncommon in watching a bolus pass down the neck of the horse to see it suddenly come to a standstill, and then slowly pass on again after probably an attempt to ascend. This is generally due to absence of saliva. In rumination and in vomiting the wave runs upward from the stomach to the pharynx. Division of the vagus interferes with the passage of food along the œsophagus, which in consequence becomes blocked.

The Saliva.

During the process of mastication the food becomes mixed in the mouth with a fluid known as saliva, the secretion of which occurs in three distinct pairs of glands. The method by which it is formed is important to understand, as much the same process occurs in other secretory glands which we have not the same opportunity of watching during their activity.

Classification of Salivary Glands.—The three glands which secrete saliva are the parotid, submaxillary, and sublingual; these are structurally divided into two groups, mucous and serous (or albuminous) glands, the submaxillary and sublingual being types of the first, the parotid the type of the other.

The following table from Colin shows the relative proportion of the glands in various animals :

	Horse.	Ox.	Sheep.	Pig.	Dog.
Parotid - -	78·00	45·00	52·00	81·00	48·00
Submaxillary -	17·00	48·00	43·00	16·00	52·00
Sublingual - -	00·05	00·07	00·05	00·03	—
	100	100	100	100	100

The table shows that, excepting the pig, the horse has the best-developed parotid system, while his submaxillary glands are very small. With the ox the parotid and submaxillary glands are nearly equal in weight. Colin showed that the size of a salivary gland does not determine its secretory power ; the parotid of the horse secretes from fifteen to twenty times more saliva than the submaxillary, while it is only about five times heavier. Similarly the parotid of the ox secretes four times more saliva than the submaxillary, though they are nearly of equal weight.

All the salivary glands belong to the class known as 'compound tubular.' The parotid is regarded as the type of serous (or albuminous) gland, and this holds good in all animals; but the submaxillary is sometimes of the mucous type, as in the dog and cat, and sometimes mixed, as in man. The sublingual may also be a mixed gland, though with mucous cells predominating.

Mucous glands are generally characterised by the presence of peculiar crescent-shaped cells known as *demilunes*, lying beneath the basement membrane, and away from the central lumen of the tube. Great difference of opinion has existed as to the special function of these *crescents of Gianuzzi*, some believing that they replace worn-out mucous cells, others that they possess specific functions.

It has been supposed that the activity of the three glands depends upon the character of the food substances, and in the dog there is experimental proof of the correctness of this view. Pawlow, whose work on digestion has opened up a new field, has shown that in the dog—and the following remarks refer solely to this animal—the submaxillary gland responds to the sight of food, to the chewing of meat and the action of acids; while the parotid responds to dry food, such as dry powdered meat, bread, or biscuit.

The selective power of the glands and their adaptability to the class of food in the mouth is very remarkable. Dry bread excites the parotid, since water is required to moisten it, and the submaxillary since mucin is needed in order to lubricate it, but moist bread only stimulates the submaxillary. Fresh meat requires no parotid, but only submaxillary saliva. Pebbles placed in the mouth excite little or no secretion, but pebbles reduced to sand excite an abundant secretion. It has been suggested that in this experiment the abundant secretion is to wash out the sand, while pebbles require no washing out, as they can be dropped. Still more remarkable, it has been shown that the *sight* of dry food causes an abundant secretion of watery saliva and a flow of rich, mucinous saliva.

From this it is evident that no stimulation of the buccal mucous membrane is essential to secretion, though there can be little doubt that the adaptative mechanism is frequently provoked through this channel.

In the herbivora Colin was able to show that the secretion of saliva was uninfluenced by the sight or smell of food; nor could he obtain any secretion from the parotids by the employment of excitants to the mucous membrane of the mouth; salts, acids, aromatic substances, were all equally negative in this respect. The submaxillary and sublingual glands, on the other hand, actively responded to these stimuli. In the horse he found that oats produced a greater secretion of saliva than hay, though the amount of fluid absorbed by oats is one-quarter that of hay.

It is well known in the human subject that fear or anxiety gives rise to impulses inhibiting secretion of saliva ; the mouth becomes dry, and the tongue refuses to move. In the horse an identical condition is produced by abdominal pain. During an attack of colic the mouth is quite dry, which symptom is of the utmost value. The dryness is not due to thirst, for the animal never drinks while the pain lasts ; a moist condition of mouth and a desire for water are two favourable indications of the utmost value in prognosis.

Physical and Chemical Characters.—Mixed saliva is an alkaline, opalescent, or slightly turbid fluid which readily froths when shaken. On standing exposed to the air, it throws down a deposit of carbonate of lime due to the loss of its carbonic acid. It has a specific gravity of 1005 in the horse, and 1010 in the ox. Examined microscopically, saliva is seen to contain epithelial scales and salivary corpuscles. The latter are small round granular cells which seem to be altered leucocytes, and are probably derived from the soft palate. About 0·6 per cent. of the saliva consists of mineral matter, and 0·2 per cent., more or less, of organic matter, the latter consisting of mucin (which gives saliva its well-known viscidity and ropiness), and small amounts of proteid substances the nature of which has not been exactly determined. Mucin belongs to a peculiar group of proteid bodies combined with a carbohydrate, for which see Chapter XX. Ptyalin or salivary diastase is the most interesting organic constituent of saliva in man, and belongs to a group of ferments known as unorganised. It is doubtful if it exists in the herbivora, and under any circumstances its amount has not been determined. Ptyalin is also absent from the saliva of the dog. The salts of saliva are principally carbonate of lime, alkaline chlorides, and phosphates of lime and magnesia. A substance known as sulphocyanide of potassium has been found in minute quantities in the saliva of the human subject, but is absent from that of the horse. The gases of the saliva are principally carbonic acid, with traces of oxygen and nitrogen ; there is no body fluid which contains so much carbonic acid as saliva (65 volumes per cent.). The three salivas have different physical properties : Parotid saliva is watery, clear, and free from mucin, but contains a small quantity of proteid ; submaxillary and sublingual saliva are viscid, especially the latter, owing to their richness in mucin. The watery saliva is to impregnate the food and prepare it for digestion, but the viscid salivas are principally concerned in swallowing.

Amount of Secretion.—Colin observed some remarkable facts regarding the secretion of the various salivary glands in the herbivora. When an animal is masticating, the parotid on that side is secreting, while its fellow is practically resting. When the rhythm of mastication changes over to the opposite side, the parotid on that side becomes active, while the other passes into the condition of comparative rest. The parotid of the side on which the animal is masticating will secrete two, three, or four times as much saliva as its fellow. The following table shows one of Colin's experiments on the horse :

	Right Parotid.	Left Parotid.	Direction of Mastication.
	Grammes.	Grammes.	
3 minutes	50	110	To the left
6 ,,	200	50	To the right
4 ,,	30	100	To the left
5 ,,	200	30	To the right

So far, these observations apply both to the horse and ruminant, but differences soon occur. When the horse is no longer eating, the parotids stop secreting, but with the ruminant this is not the case : the parotids continue to act, not only during rumination, but during abstinence. During rumination the secretion is unilateral in the sense that very much more is obtained from the side on which the jaws are active.

The secretion from the submaxillary and sublingual glands behaves quite differently to that of the parotid. It is constant from both sides in all herbivora, no matter what the direction of mastication may be. The submaxillary glands cease to secrete during rumination ; the sublingual is not affected by this function.

The actual amount of fluid secreted daily from these glands in the large herbivora is astonishing. Colin put it down at 5 to 6 kilogrammes (8½ to 10½ pints) hourly for the horse during the seven hours he is engaged in feeding. He gives the total daily secretion for the animal at 42 kilogrammes (9¼ gallons), while for the ox it is still higher—56 kilogrammes (12¼ gallons), of which from 800 grammes (1·4 pints) to 2,400 grammes (4¼ pints) are produced per hour during the intervals of feeding. The submaxillary secretion is placed at 280 grammes (1½ pints) per hour, and the sublingual at 18 to 20 grammes (¾ ounce) per hour.

It is obvious that the amount of secretion depends upon the character of the food ; only half the daily mean is secreted if green food be given, and only one-third if roots form the diet. On the other hand, oats increase the amount secreted. Hay absorbs four times its weight of saliva, oats a little more than their weight, and green fodder half its weight.

The **use of the saliva** in herbivora is to assist in mastication and swallowing, stimulating the nerves of taste, and in ruminants assisting in rumination. According to the writer's observations on the horse, saliva has no chemical action on the raw starch of its food, and this is not surprising when we remember that the starch grains are enclosed in an envelope of cellulose, a substance on which saliva has no action. So intimately, however, is salivary secretion associated with starch conversion, that it is not possible to pass over without further notice the action produced on starch in man, and, according to some observers, in horses and cattle, by the presence of ptyalin in the saliva.

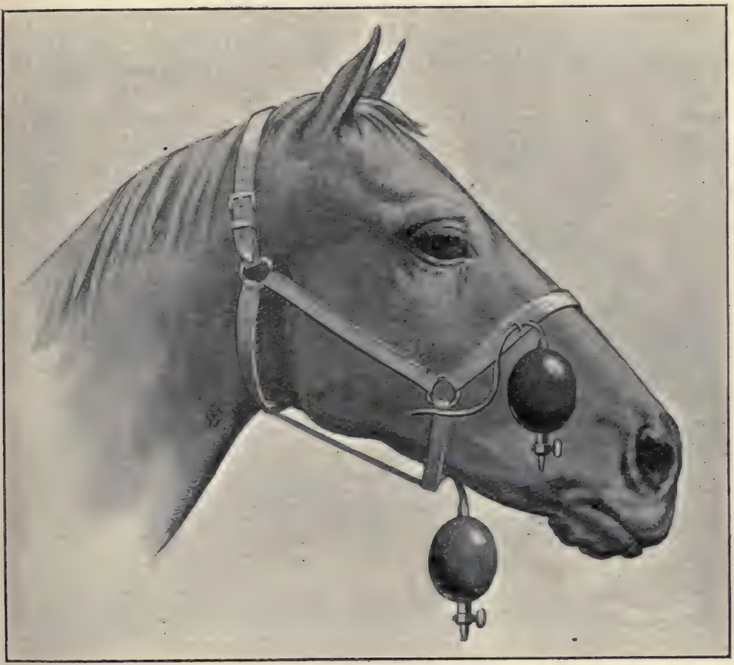

Fig. 58.—Apparatus employed by Colin in Experiments on the Secretion of Parotid and Submaxillary Saliva.

The **starch** found in plants exists in the form of granules possessing a shape peculiar to the species; these granules are enveloped in a tough envelope of cellulose; before the true starch, the *granulose* contained in the cellulose envelope, can be reached the cellulose must be traversed. For this reason some animals, like man, cannot digest raw starch, but by cooking, the starch (granulose) is liberated and free to be acted upon;

on the other hand, all the herbivora are capable of digesting raw starch, perhaps because they can digest cellulose.

If boiled starch be mixed with filtered human saliva and kept at a temperature of 95° F., in a short time the characteristic reaction of a blue colour with iodine disappears, and a reddish colour is formed on the addition of this reagent, indicating the presence of a substance known as **erythrodextrin.** The fluid, which before was sugar-free, contains distinct evidence of the presence of this substance ; by continuing the action of the saliva it is shortly found that the red colour on the addition of iodine has disappeared, and the fluid gives evidence of containing a considerable proportion of sugar. But analysis shows that for the amount of starch employed the full amount of sugar has not been obtained ; in other words, there is a second substance present besides sugar, which is produced as the result of the action of the saliva, and to this the name **achroodextrin** has been given ; it is formed from erythrodextrin. The sugar formed from starch by the action of saliva is not grape-sugar, but maltose ; glucose (dextrose or grape-sugar) only being found in small quantities, if at all. This action of the saliva on starch is described as the **Amylolytic** action ; it is due to the presence of ptyalin.

Ptyalin, the active principle of starch-converting salivas, is an unorganised enzyme, and, like all ferments, is of unknown chemical nature. It is capable of converting cooked starch rapidly and raw starch slowly into maltose and dextrin, the ferment acting by hydrolysis ; viz., the molecule of starch takes up water, and undergoes cleavage into simpler bodies. Between starch and maltose there are doubtless many other bodies, but the chemistry is not agreed upon. The amylolytic action is permanently destroyed by a high, inhibited by a low temperature, retarded by a slightly acid or alkaline medium, and destroyed by free hydrochloric acid. If starch be boiled with a dilute acid, conversion into sugar occurs. The difference between the action of boiling acid on starch and of saliva is that the latter can only produce maltose, whereas the acid produces dextrose.

The view we hold as to the non-amylolytic action of saliva in herbivora is not supported by other observers ; Ellenberger* distinctly states that both the parotid and submaxillary secretions of the horse and ox can convert starch into sugar, but in the case of the horse it is only the saliva first secreted by the glands after a rest which possesses this property ; as secretion proceeds the power is nearly lost. In the pig, according to this observer, all the salivary glands are starch-converting ; in the rabbit the submaxillary has no action, while the parotid is energetic ; in the cat, dog, horse, sheep, and ox the action is very feeble or entirely absent. Meade Smith* states that the saliva of the horse will convert crushed raw starch into sugar in fifteen minutes, and that the process is continued in the stomach ; he further adds that the saliva of the horse will convert cane into grape sugar. In ruminants he believes starch conversion takes place both in the mouth and rumen. Though we do not accept these views, we shall shortly endeavour to show how starch is converted into sugar in the stomach of the horse. It is interesting in this respect to note that in man starch conversion, brought about by the action of ptyalin, is also now recognised as taking place in the stomach from the swallowed saliva—in fact, that the bulk of the conversion must necessarily take place there, and not in the mouth.

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* 'Physiologie der Haussäugethiere.'

Secretion of Saliva.—The mechanism concerned in the secretion of saliva deserves careful attention, for the reason that it throws considerable light on other secretory processes. The subject has been worked out by so many competent observers that the leading points are beyond all doubt ; the submaxillary gland of the dog has mainly afforded the desired information, and there is reason to believe that the same process holds good for the parotid and other glands, both of this animal and of herbivora.

The chief point in the secretion of saliva is that it is controlled by the nervous system, and is not directly dependent upon any mere increase in the blood-pressure in the gland. Afferent nerves—viz., the gustatory division of the fifth and the glosso-pharyngeal—convey from the mouth to the medulla a certain impulse, which, by means of efferent nerves, is conveyed to the gland, and secretion results. The efferent nerve of the submaxillary gland of the dog is supplied by the **chorda tympani,** a small branch given off by the seventh cranial nerve, which enters the gland at its hilum, and supplies the vessels with dilator and the cells with secretory fibres. The second nerve supplying the submaxillary gland is a branch of the **sympathetic,** which spreads out and invests with constrictor fibres the walls of the artery supplying the part (Fig. 59). Thus the chorda tympani supplies the gland with secretory fibres and the walls of the vessels with dilator fibres, while the sympathetic supplies the vessels with constrictor fibres, and only a few secretory fibres.

If the tongue or the lingual branch of the fifth or glosso-pharyngeal nerves be stimulated, secretion of saliva results ; if the sympathetic nerve be divided and the tongue then stimulated, secretion follows ; but if the chorda tympani be previously divided, no secretion follows on stimulation of the tongue, lingual, or glosso-pharyngeal nerves. If the chorda be stimulated, the vessels dilate, the gland becomes red, the blood flowing from the veins is arterial in tint, and the veins pulsate ; in addition to this, there is an abundant secretion of watery saliva poor in solids. When the sympathetic is stimulated, exactly the reverse is observed—viz., the vessels constrict, in consequence of which the gland becomes pale, only a small quantity of extremely viscid saliva flows, which is rich in solids, the blood in the veins becomes very dark in colour, and the blood-stream slows to such an extent that if the veins leading from the gland be cut, the flow from them is less than from a gland at rest. That the increased flow

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* 'Physiology of the Domestic Animals.'

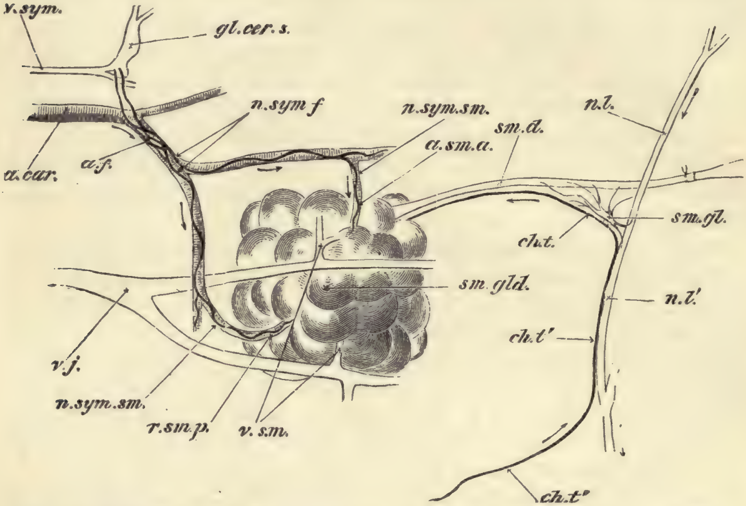

FIG. 59.—DIAGRAMMATIC REPRESENTATION OF THE SUBMAXILLARY GLAND OF THE DOG, WITH ITS NERVES AND BLOODVESSELS (FOSTER).

(The dissection has been made with the animal on its back, and is very diagrammatic.)

The submaxillary gland (*sm. gld.*) occupies the centre of the figure ; the bloodvessels supplying it, derived from the carotid artery, *a.car.*, are seen on the left, whilst the duct from the gland *sm.d.*, in which a canula is inserted, is on the right of the figure.

The chorda tympani nerve, *ch.t''.*, running in company with the lingual branch of the fifth *n.l'.*, is seen to the right and below ; after running together the two nerves separate, the chorda tympani, *ch.t.*, running along the submaxillary duct to the gland. Close to where the two nerves separate is the submaxillary ganglion, *sm.gl.*

The sympathetic nerve-supply is shown in the figure to the left and above, the fibres being derived from the superior cervical ganglion, *gl.cer.s.*, and coursing along the bloodvessels to enter the gland.

The bloodvessels leading from the gland fall into the jugular vein, *v.j.*

The arrows indicate the direction of the nervous impulses during the reflex act, ascending to the brain by the lingual, and descending by the chorda.

of blood to the gland produced by stimulating the chorda is not the essential cause of the secretion, is proved by the fact that the pressure of the saliva in the duct of the gland is higher than the blood-pressure within the vessels. Further, if before stimulating the chorda some *atropine* be injected, stimulation of the nerve still produces to the full all the vascular changes, but not a trace of saliva is secreted. Hence, secretion is not due merely to increased blood-pressure. This atropine experiment proves the existence in the chorda of two sets of nerves—viz., secretory and vaso-dilator ; owing to the action of atropine, the secretory nerves are paralysed, while the vaso-dilators are not. And in the sympathetic two sets of nerves can similarly be demonstrated—secretory and vaso-constrictor—though it is most likely that in the majority of animals the secretory fibres in the sympathetic are few in number. *Pilocarpine* is antagonistic to atropine, and produces a profuse flow of saliva.

A peculiar phenomenon is observed in connection with salivary secretion after division of the chorda. Though the gland is cut off from its secretory nerve, yet one or two days after section a secretion appears, and may continue for some weeks until the gland undergoes atrophy. This is known as 'paralytic secretion.' The cause of paralytic secretion is not definitely known. The cut portion of nerve in connection with the gland degenerates ; it has been suggested that the secreting cells are controlled by inhibitory fibres in the nerve, and that the cells, in consequence of a local nervous mechanism in the gland, continue secreting. Very little of a definite nature is known of the paralytic phenomenon, and it is curious to observe that it is not limited to the gland of which the nerve has been divided, but affects both sides. Langley, who has described this, refers to the continuous secretion from the unoperated gland as *antiparalytic* or *antilytic*.

Heidenhain's view of the action of secretory nerves is that a gland is supplied with a trophic or nutritive nerve which excites the formation of the organic constituents of the secretion, and a secretory nerve which controls the secretion of water and inorganic salts. The cranial nerves are chiefly secretory, while the sympathetic are trophic, or building up ; hence stimulation of the chorda yields the water and salts of the saliva, while stimulation of the sympathetic produces the organic substances and ferment.

Trophic fibres are supposed to effect a breaking-down of the complex living substance of the gland and conversion into simpler bodies, and that chemical changes of importance are occurring is undoubted from the large amount of CO_2 found in saliva, which indicates active oxidation. Saliva contains more CO_2 than any other secretion of the body—more, even, than venous blood. Side by side with the above destructive changes construction must also be going on, though there are no known nerve fibres responsible for the process. As to the manner in which the secretory nerves act very little is known ; the blood loses more water than can be accounted for by the amount in the saliva, the difference being supposed to be represented by an increase in the lymph flow from the fluid ; but in what way nerve impulses can cause the cells to secrete is at present inexplicable.

The method by which secretion in the parotid gland is carried out differs in no essential respect from that of the submaxillary. The nerves supplying the parotid are the glosso-pharyngeal (the action of which corresponds to the chorda of the submaxillary) and the sympathetic. In the glosso-pharyngeal are dilator fibres, and in the sympathetic constrictor fibres for the blood-vessels, while both trunks contain secretory nerves.

The influence of atropine and pilocarpine on the gland-cells has previously been mentioned ; it remains to notice the effect of *nicotine,* which prevents the secretion of saliva—not, however, by its action on the gland-cells, but by paralysing the connections of the nerve fibres in such ganglia as the submaxillary, Langley's, and the superior cervical. This action of nicotine, which essentially consists in paralysing the *nerve-cells* in the ganglia, and not the fibres, was discovered by Langley, and has largely helped in building up our knowledge of the sympathetic system.

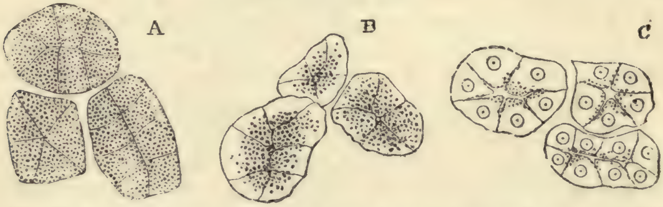

FIG. 60.—CHANGES IN THE CELLS OF THE LIVING PAROTID (SEROUS GLAND) DURING SECRETION (FOSTER, AFTER LANGLEY).

A, At rest ; B, in the first stage of secretion ; C, after prolonged secretion.

The **changes occurring in the cells** of the salivary glands during secretion depend upon the type of gland. We select Langley's observations, since he examined the living gland, and not one simply hardened and stained. During the stage of rest in a living serous gland, such as the parotid, the cells are found to be filled with a quantity of granular material, and the outline of each individual cell is indistinct ; the lumen of the gland is also occluded, and no nucleus can be observed in the cells ; in other words, the gland is charged with its secretory products (Fig. 60, A).

During activity the cells get rid of their granular material, which gradually passes towards the centre of the acinus or lumen, leaving each cell with a clear outer edge, while that edge next the lumen is still granular (Fig. 60, B). In an exhausted condition the cells are smaller and remarkably clear, only a few granules being left in them on the inner edge, while the lumen is now distinct and large, and the nuclei are clearly seen occupying a central position (Fig. 60, C).

If a mucous gland, such as the submaxillary, be examined at rest under like conditions, the cells are found filled with granules much larger than those of a serous gland, and a nucleus is seen occupying one edge of the cell (Fig. 61, a). During activity the granules are passed into the lumen of the gland, but they do not leave behind them in the cells the same clear space seen in the serous cell (Fig. 61, b). If the cells, while in an active condition, be acted upon by water or dilute acetic acid, the granules swell up and become transparent owing to the mucin they contain, and a delicate network is seen to pervade the cell (Fig. 61, a′). A similar appearance is produced in the exhausted cell (Fig. 61, b′), excepting that less transparent mucin is seen and more granular substance, while the nucleus of the exhausted irrigated gland is seen passing towards the centre of the cell instead of remaining close to the outer wall. Though we have spoken of these granules as mucin, in the gland they are not really mucin, but the mother-substance of it—viz., *mucigen*—which during the act of secretion is converted into mucin. The same holds good for the serous type ; the granules in the resting gland are the precursors of the ferment or the *zymogen* of the secretion, from which the secretion is actually formed at the moment it is poured out.

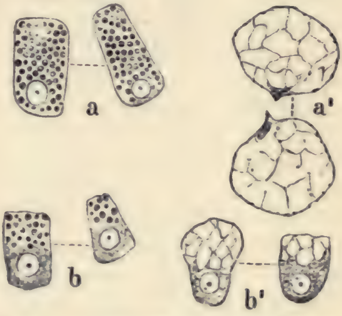

FIG. 61.—CELLS FROM MUCOUS GLAND (SUBMAXILLARY GLAND OF THE DOG) (FOSTER).

a, From loaded gland ; b, from discharged gland ; a′, b′, treated with dilute acetic acid ; a′, from loaded ; b′, from discharged gland.

The outcome of the changes above described proves that the organic elements found in the salivary secretion are manufactured by the cells in the glands ; the inorganic constituents are either the result of filtration or secretion. Experiments made by Langley and Fletcher go to prove that even water and salts are the result of an act of cell-secretion, and not of mere transudation.

SECTION 2.

Stomach Digestion.

Important digestive changes in the food of the lower animals take place in the stomach. It is not a matter for surprise to find that the size and shape of this organ varies with the species of animal; we should expect to meet with a simple stomach in the dog, and complex arrangement in vegetable feeders. It seems remarkable that any animal should possess a laboratory capable of converting grass, hay, and grain into muscle and fat; and it is evident that the conversion of vegetable into animal tissues must be a more complex process than the conversion of animal tissues into the living structure of an animal body. But it is curious to observe that a complex stomach for a vegetable feeder is by no means a necessity; the stomach of the ruminant and the simple stomach of the horse could not be in greater contrast, while the resulting laboratory processes are practically identical. So far as vegetable food is concerned, it does not matter whether the solution and absorption of its readily soluble matters comes before maceration, or whether maceration precedes the extraction of the readily soluble substances. If maceration comes first, as in ruminants, bulky gastric compartments are provided for the purpose, and the subsequent intestinal canal is small. If the simple stomach comes first, bulky intestines for the purpose of maceration follow; in both cases ample provision is made for the maceration necessary for the solution of the cell wall and fibrous portion of plants. The dog, with its simple stomach and simple intestines, offers no difficulty to our understanding. He lives on flesh, and converts it into flesh; it is not very clear why he has both a stomach and intestines, for the whole process of digestion is simple, and could be readily carried out single-handed by the intestines. In fact, the stomach of the dog has been removed experimentally, and the animal remained in health.

For simplicity in construction the stomach of the dog occupies one end of the scale, for complexity the gastric reservoirs of the ox occupy the other, while between the two comes the stomach of the omnivorous pig, partaking of some of the characters of the carnivora and ruminant, and belonging to neither.

Stomach Digestion in the Horse.

The subject of stomach digestion in the horse has been worked out by means of feeding experiments, as it has been found impossible to establish a gastric fistula in this animal owing to the distance the stomach lies from the abdominal wall; pure gastric juice has, therefore, never been obtained from the horse.

The first peculiarity to be noticed in soliped digestion is that the stomach is rarely empty; it is only when horses have purposely been deprived of food for not less than twenty-four hours that an empty stomach can be obtained. On the other hand, feeding experiments show that very shortly after food arrives in the stomach it commences to pass out, and the difficulty thus presented to the observer in reconciling these opposed facts is at first sight considerable. It is perfectly true that food does pass out early, it is equally true that it is long retained, these opposite conditions being the result of the periods of digestion. When food enters an empty stomach, it passes towards the pylorus, where it meets with a fluid of an alkaline or neutral reaction which has come from the mouth. As more food is consumed an acid fluid is secreted in the stomach, and material commences to pass out at the pylorus into the bowel, the amount passing out not equalling at present the amount passing in. Thus the stomach becomes gradually distended, and when two-thirds full, which is the condition in which the most active digestion occurs, the amount passing out will, if more food be taken, equal the amount being swallowed, so that we have a stream of partly peptonised chyme streaming out of the right extremity, while a corresponding bulk of ingesta is entering the inert left sac. In fact, the stomach may during feeding allow two or three times the bulk of food to pass out which remains in it when the meal is finished. No sooner is the feed finished than the passage of chyme into the duodenum ceases, or becomes so slowed down that only small quantities of food pass out, and so gradually does this occur that it will be many hours before the stomach is really empty, though had the process continued as it commenced, it would not have contained anything at the end of an hour. This condition of stomach digestion in the horse may be variously modified, depending on the nature of the food, the quantity given, the form in which it is given, the order in which one food follows another, and whether water be given before or after feeding. All these are points requiring our attention, but before giving it we must briefly look at the stomach itself.

The mean capacity of a horse's stomach is, according to Colin, from 15 to 18 litres (3 to 4 gallons); these figures were obtained from a very large number of observations, and give the extreme size of the organ when distended. The viscus is under the best physiological conditions for digestion when it contains about 10 to 12 litres (2 to 2·5 gallons), or is distended to two-thirds of its capacity. The mucous membrane of the stomach of the horse is peculiar ; one portion of it, practically half, is a continuation of the membrane of the œsophagus ; this ends abruptly, and is succeeded by the villous coat, which extends to the pylorus. It is in this latter coat that a true digestive juice is secreted, though not from the entire surface, for on examining the villous membrane it is found to differ greatly in appearance, the fundus being channelled, furrowed, and velvety, whilst the pyloric portion is smooth. It is in the fundus only where true gastric juice—viz., pepsin and acid—is secreted ; in the smooth pyloric mucous membrane only pepsin is formed. The area of the fundus-secreting surface is about 1 square foot. Fig. 62 shows the relative position of the various parts of the mucous membrane of the stomach of the horse ; the drawing accurately indicates the shape of the stomach, the position of the inlet and outlet, and the direction and position of the various areas. In Fig. 63, after Ellenberg and Baum, is indicated the position of the organ in the living animal.

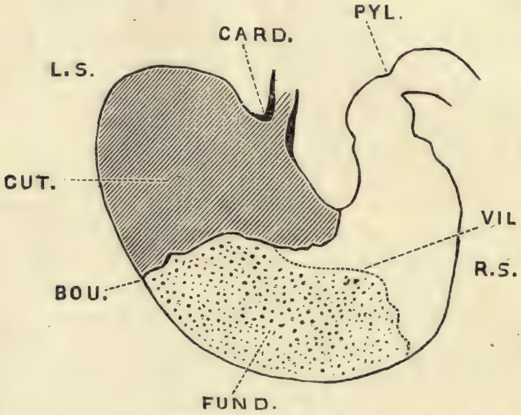

Fig. 62.—Longitudinal Section of the Stomach of the Horse.

card., Cardia ; pyl., pylorus ; l.s., left sac ; r.s., right sac ; cut., cuticular coat ; vil., villous coat ; bou., boundary line between the cuticular and villous portions ; fund., fundus of the stomach. The dotted surface indicates the area for the secretion of gastric juice.

There is a want of agreement in the matter of stomach nomenclature. The human physiologist describes the fundus of the stomach as being close to the cardia, whereas we have spoken of it as being at the bottom or on the floor of the stomach, as if it were in the position the name 'fundus' would assign it.* In

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* The fundus of an organ is the rounded base of a viscus ending in a neck, and having an aperture. It is the bottom of anything.

Fig. 64 are shown the parts of the human stomach according to modern nomenclature. To the left of the figure is seen the *antrum pylori*, marked off by a fissure, IA, and a transverse band for the main body of the organ. The main body is divided into fundus and prepyloric region; it will be observed that the position assigned to the fundus of the human stomach is not that found in the horse. On the other hand, the antrum pylori of the horse is as well marked as in the human, possessing both the transverse band and the sacculated condition towards the duodenum.

A very remarkable amount of mucin is secreted by the villous sac of the stomach, and forms over the inner surface of the viscus a thick [gelatinous, firmly adherent coating like white of egg, which cannot be washed away even by a powerful jet of water.

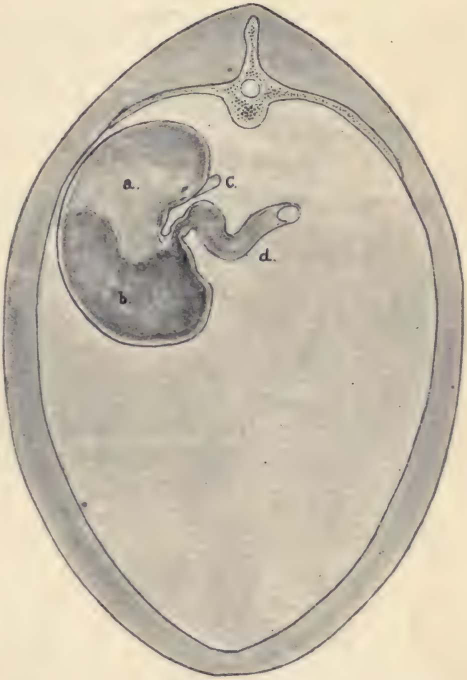


FIG. 63.—POSITION OF THE STOMACH OF THE HORSE IN THE LIVING ANIMAL (AFTER ELLENBERGER AND BAUM).

a, Vertical transverse section of the frozen body made through the fourteenth dorsal vertebra, showing the position occupied by the stomach; *c*, œsophagus; *d*, duodenum; *a*, cuticular area; *b*, villous area. As a perfectly vertical section would not give a complete picture of the stomach, owing to its obliquity, the above has been schematically amended. The observer is looking towards the animal's head.

The pyloric orifice of the stomach is usually large and open, and there is a distinct pyloric ring; behind this the duodenum is dilated, and the gut comports itself in such a singular manner (which has a very important bearing on the pathology of the organ) that mention must be made of it here. From the pylorus the duodenum curves down and then up again, forming a letter **U**; so much does this remind one of a well-known form of trap used in drainage, that we have described it as the syphon trap of the duodenum (Fig. 65). The use of this trap appears to be to regulate the passage of material from the stomach into the intestines. The writer's observations have shown that its presence in all probability influences rupture of the stomach, for the more distended the large bowels become, the greater the pressure exercised on the duodenum, and in cases of severe tympany the passage from the stomach to the intestines is completely cut off. Should fermentation still continue in the stomach, the contents can neither escape into the œsophagus, nor into the bowel, and the coats of the viscus may be completely ruptured under the intense strain. Figs. 62 and 63 demonstrate the position the greater curvature of the stomach occupies towards the left ribs. There is no space left into which the stomach can swell. It is held back by the diaphragm, pushed forward by the intestines, bound down by the ribs, and rupture of the greater curvature follows. It was mentioned on p. 159 that the œsophagus of the horse near its termination changes from red to pale muscle, and for several inches increases enormously in thickness. It is this thickened contracted end of the œsophagus which completely seals the stomach anteriorly;

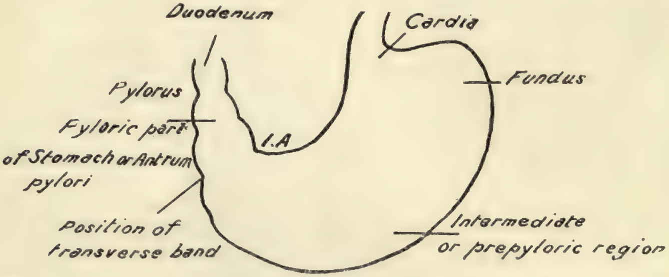

Duodenum
Cardia
Fundus
Pylorus
Pyloric part of Stomach or Antrum pylori
I.A
Position of transverse band
Intermediate or prepyloric region

FIG. 64.—SCHEMATIC FIGURE OF THE HUMAN STOMACH (HOWELL, AFTER RETZIUS).

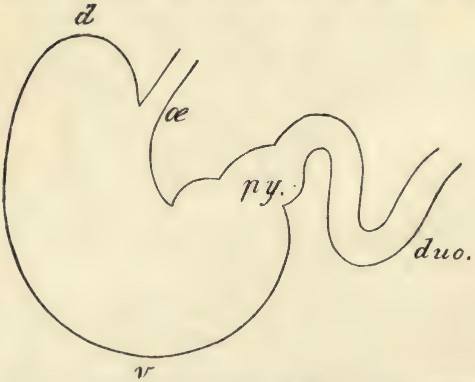


FIG. 65.—LONGITUDINAL SECTION OF THE STOMACH OF THE HORSE, SHOWING THE SYPHON TRAP OF THE DUODENUM.

œ, Œsophagus; *py.*, pylorus; *d*, left sac; *v*, fundus; *duo.*, duodenum.

nothing can be forced out by this passage, not even after death or under great pressure.

The physiological points of interest in the structure of the horse's stomach are: (1) That it is small; (2) that it is not in contact with the abdominal wall, but rests on the colon; (3) that the outlet and inlet are situated close together; (4) that the cardia is tightly constricted; (5) that only a portion of its surface is capable of secreting a digestive fluid; (6) that there are remarkable differences in the character and nature of the various regions of its mucous membrane.

We can now consider the stomach digestion of the two chief foods used for horses—viz., hay and oats.

Digestion of Hay.—Hay, as has been stated, mixes in the mouth with four times its bulk of saliva, and after a very perfect grinding passes into the stomach. If the stomach be empty it is of no size, and the material lies in the lesser curvature and pyloric region; as the viscus gradually fills, the greater curvature is occupied, the gastric juice begins to act, and chyme commences to pass into the intestines probably in a very imperfectly elaborated form. Assuming the animal to have finished eating hay, we now find the output into the intestine becomes small and slow. The gastric juice has an opportunity of acting more thoroughly upon the ingesta, which turn yellow on that surface which is in contact with the villous wall, the compression of the stomach on the contents causing them to become distinctly moulded into a mass the shape of the viscus. Owing to gravity there is more fluid towards the pylorus than elsewhere, and for the same reason the greater curvature in all probability is fuller than the lesser. The material in the stomach is perfectly comminuted, resembles firm green and yellow fæces, and the smell is peculiar, like sour tobacco. The yellowness is due to the gastric juice, and is consequently more marked towards the pylorus; the portion coloured green is the part as yet unacted upon by the juice. The entire surface of the stomach and its contents are now acid, excepting at the cardia, where it may occasionally be alkaline from swallowed saliva; the acidity is greater at the fundus than at the cardia. This general acidity shows that a diffusion of the gastric juice must have been going on. There is no evidence of any churning motion; the cake-like condition into which the hay is compressed is produced by the simple compression of the stomach walls.

The duration of hay-digestion in the stomach is very variable. In examining a series of digestions hour by hour, such as will be mentioned presently, moderately uniform results may be obtained, but even these are sure to be here and there broken by excessive, or conversely by very small, digestions which cannot be explained.

No one can say with any degree of certainty how much hay a horse will digest in any given period, as may be seen from the following observations :

	Amount digested per Cent.
After 4¾ hours' digestion	17
,, 5 ,, ,,	66
,, 5½ ,, ,,	64
,, 6 ,, ,,	44
,, 9 ,, ,,	58

It is known, however, that as a rule more will be digested in the first hour, less in the next, still less in the third, and so on until the stomach empties itself, or until what exists in the stomach is actually pushed out by the arrival of the next feed. Assuming, however, that the animal is purposely starved, the stomach may not empty itself for fifteen, eighteen, twenty-four, or even thirty-six hours. It is impossible to say, either at the end of twelve or of thirty-six hours, that the stomach has passed the whole of its contents into the intestine. The writer has found hay in the stomach fifteen and eighteen hours after being given, and under identical experimental conditions the stomach at the fifteenth hour has been found empty.

Colin's elaborate researches furnish very complete data on the question of hay digestion in the horse. In one experiment carried out on fourteen animals he divided them into two groups, each horse receiving 2·5 kilogrammes (5·5 pounds) hay. One group had long, the other chaffed hay. The following table shows the percentage digested at each period :

	Long Hay.	Chaffed Hay.
	Per Cent.	Per Cent.
Amount digested at second hour	61	56
,, ,, third hour	69	77
,, ,, fourth hour	73	64
,, ,, fifth hour	78	91
,, ,, sixth hour	74	83
,, ,, seventh hour	73	79
,, ,, eighth hour	88	81

This shows that the rate of digestion falls off after the second hour, so that even at the end of eight hours there is still food left in the stomach. Only one animal digested as much as 90 per cent., and this was at the fifth hour. With this exception the results are fairly uniform, and they further demonstrate that chaffing hay does not increase its rate of digestion.

The influence of water on the digestion of hay was tested by Colin. The following table shows the results, and also furnishes detailed information, hour by hour, of the rate of stomach digestion :

Duration of Digestion.	Hay without drinking Water (per Cent. digested).	Duration of Digestion.	Hay with drinking Water (per Cent. digested).
Hours.		Hours.	
½	30	1½	41 (mean of 2 experiments)
1	45	2	46 ,, 4 ,,
2	37 (mean of 4 experiments)	3	61 ,, 2 ,,
3	52	4	64 ,, 5 ,,
5	77	5	88 ,, 3 ,,
6	66	6	79 ,, 3 ,,
7	64	7	87
8	72	9	82 ,, 2 ,,
10	83	10	92 ,, 2 ,,
11	95	11	95
12	95	12	85 ,, 2 ,,
14	96	13	92
18	96	14	94
		15	97
		16	98

On the whole, during the earlier hours of digestion the horses receiving water digested hay better than those kept without it, but there is no difference after the ninth or tenth hour succeeding feeding.

Digestion of Oats.—Oats take up their own weight of saliva, and during digestion behave much as does hay—viz., while the animal is feeding the contents of the stomach begin very early to pass into the intestine, but the rate is considerably reduced the moment no more material arrives in the organ.

Colin fed six horses on 2·5 kilogrammes (5·5 pounds) oats : three horses received uncrushed, three crushed corn, and the following table shows the percentage digested :

Duration of Digestion.	Crushed Corn (per Cent. digested).	Uncrushed Corn (per Cent. digested).
2 hours - - -	48	45
4 ,, - - -	56	61
6 ,, - - -	62	54

The crushing of the corn made no difference to the rate of digestion—a point of practical importance in dietetics. Comparing this table with the one on p. 178, it would appear that hay is easier of digestion than oats.

The digestion of oats in individual horses is just as irregular as that of hay. A horse to which only 2 pounds of oats were given was destroyed twenty hours later, and the stomach was not completely empty. In another to which 1 pound had been given 6 ounces were recovered after four hours' digestion. In the following table the results of some experimental feedings are recorded:

	Amount digested per Cent.
3 hours	45·0
3 ,,	57·0
3 ,,	70·0
3 ,,	78·6

These horses were fed under similar conditions, yet there is a good deal of variation in the amount digested. In the next table the period of observation was increased in order to see whether greater uniformity would result:

	Amount digested per Cent.
4 hours	Nil
4 ,,	18·0
4 ,,	54·5
4 ,,	56·0
4 ,,	75·0

These results are less regular than those of the first series; one horse digested nothing, and that is explained by a practical fact capable of being turned to clinical account. The animal was of a very nervous disposition, and the experiment was carried out in a strange stable, the mare being alone, whereas she was used to the company of other animals. The second horse in this series only digested 18 per cent.; this also illustrates a practical point in feeding—namely, the influence of a sudden change in diet. This animal had not received oats for eighteen months, having been fed on a patent food; the sudden change to oats for the experimental observation explains why only 18 per cent. had been digested.

Arrangement of Food in the Stomach.—If a horse be fed on oats, maize, hay, etc., in succession, the stomach, on examination, will be found to contain these substances quite unmixed, and arranged in strata in the order of their arrival, the first food being in the pylorus and greater curvature, the last in the cardia and lesser curvature. We have pointed out that the contents of the stomach of the horse are squeezed and pressed, but never churned. In successive feeding the material never mixes, excepting at the pylorus, but keeps together from the time of its arrival until it passes out of the stomach, a sharp line of demarcation distinguishing it from its neighbour. If the stomach be empty or greatly contracted, the first food to arrive is lodged in the lesser curvature and pylorus; gradually, as new material arrives, this passes over to the greater curvature in order to make room for it. If a horse be fed first with hay, followed by oats, the presence of the oats causes the hay to pass out more rapidly than it would have done had it been given alone.

Ellenberger has shown that when hay and oats are given in the order named, a portion of the oats may pass into the bowel by the lesser curvature without entering either the left sac or fundus of the stomach (see Fig. 66, I.). When oats followed by hay are given, the oats, as the first arrival, naturally commence to pass out first, but the presence of the hay hurries the rate of progress, and the oats pass more quickly into the intestines than they otherwise would have done. The regular arrangement of food in layers is disturbed when a horse is watered after feeding; half the food may in this way be washed out of the stomach, for the water which a horse drinks does not stop in the stomach, but passes directly through it on its way to the cæcum. Hence we have the golden rule of experience that horses should be *watered first and fed afterwards*.

These facts may be summarised by saying that in a succession of foods the first consumed is the first to pass out. That does not mean to say that the whole of it passes out before any portion of the succeeding food enters the bowel, for we have shown that after a time, at the pylorus, they mix and pass out together; but the actual influence of giving a food first is to cause it to pass out first. The practical application of this fact, according to Ellenberger, is that when foods are given in succession, the least albuminous should be given first. This appears distinctly to reverse the English practice of giving oats first and hay afterwards, but perhaps only apparently so, for experiment shows that the longer digestion is prolonged, the more oats and the less hay pass out, so that some hay (under ordinary circumstances a moderate quantity) is always left in the stomach until the commencement of the next meal. The presence of this hay from the previous feed may prevent the corn of the succeeding meal from passing out too early. According to Ellenberger, in order that horses may obtain the fullest possible nutriment from their oats, hay should be given first, *and then water*; this carries some of the hay into the bowel, and after a time the oats are to be given. The remaining hay now passes into the bowel, and the oats remain in the stomach. This does not accord with English views of watering and feeding fast-working horses, views which have stood the test of prolonged practical experience.

The appearance of the food after it has been in the stomach depends upon the period of digestion. We have previously drawn attention to the fact that an hour or two after hay has been taken the material is found in a finely-chopped condition, firm—one may almost say dry—in places, though towards the pylorus it is liquid. This hay contains between four and five parts of saliva ; it is yellow in colour where the gastric juice has

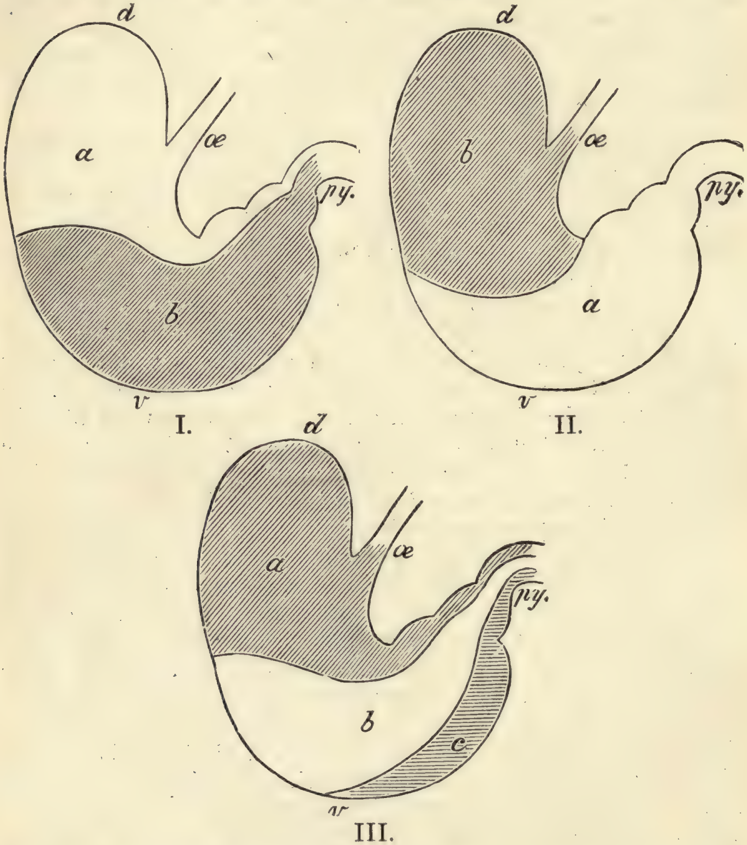


Fig. 66.—Longitudinal Section of the Horse's Stomach, showing the Arrangement of the Food according to the Order in which it was received (Ellenberger).

In each case *œ* is the œsophagus ; *py.*, pylorus ; *d*, the left sac ; *v*, the fundus. I. Hay first, followed by oats : *b*, the hay ; *a*, the oats ; the latter are passing along the lesser curvature and escaping with the hay at the pylorus. II. Oats first, followed by hay : *a*, the oats ; *b*, the hay. III. The order of three successive feeds : *c*, the first feed ; *b*, the second ; *a*, the third.

attacked it, but of rather a greenish tint elsewhere, and it has a peculiar odour. Several hours after feeding, the stomach is found to contain a variable quantity of watery fluid discoloured by the hay which is left behind, part of which may be found floating on the fluid. At other times, when the stomach is empty, the fluid is viscid, contains numerous gas bubbles, and is of an amber or yellow tint; this particular fluid is no doubt saliva and mucin, with possibly a little bile, the result of a reflux from the bowel. When oats alone have been given, the contents of the stomach are found liquid, the fluid being creamy in consistency and colour; the oats are swollen, soft, and their interior exposed; towards the end of digestion the creamy fluid is replaced by the frothy yellow one. With both hay and oats, and also other foods, there is a peculiar sour-milk-like smell from the contents of the stomach, more marked with bran and oats than with hay, the latter, as previously mentioned, smelling like sour tobacco.

The **reaction of the contents of the stomach** is strongly acid; this acid reaction may be obtained on the cuticular as well as the villous portion of the lining, and is very persistent; the cuticular membrane, even after prolonged washing, gives an acid reaction. The acidity is derived entirely from the juice secreted by the villous membrane of the fundus. Our observations on this subject do not agree with those of Ellenberger, who says that during the first hour of digestion the contents of the stomach may be alkaline; acidity, he states, then commences in the fundus and extends to the cardia, though for some time the proportion of fundus acidity is three or four times greater than that of the cardia; in the course of five or six hours the proportion of acid throughout the stomach is equal. When the stomach is empty, as after a few days' starvation, its reaction is neutral or alkaline. We have observed extreme alkalinity towards the pylorus under these conditions, due, no doubt, to the regurgitation of bile and pancreatic fluid.

Alkalinity of the contents may be met with at the cardiac end of the stomach; in such cases it is due to the swallowed saliva, and the stomach contents at this part exhibit a marked sugar reaction. It is difficult to say whether this alkalinity is invariable; in the writer's experience it has been seldom met with; but the period of digestion may be responsible, for it is easy to understand that during the early period of digestion the stomach acids will not have penetrated to the upper part of the stomach, and in this way have neutralised the immense bulk of salivated food of an alkaline reaction which is swallowed.

The Stomach Acids.—It is not necessary here to enter into any detail as to the nature of the gastric acids; both in the horse and man a considerable amount has been written to prove that the acidity depends upon lactic or hydrochloric acids, and it is possible that both these views may be reconciled. Ellenberger and Hofmeister are of opinion that shortly after a meal lactic acid predominates in the horse's stomach, to be replaced by hydrochloric acid some four or five hours after the commencement of feeding. These observers found that the nature of the acid depended upon the region of the stomach, the period of digestion, and the character of the food; oats induced an outpouring of hydrochloric acid, whilst hay favoured the organic acids.

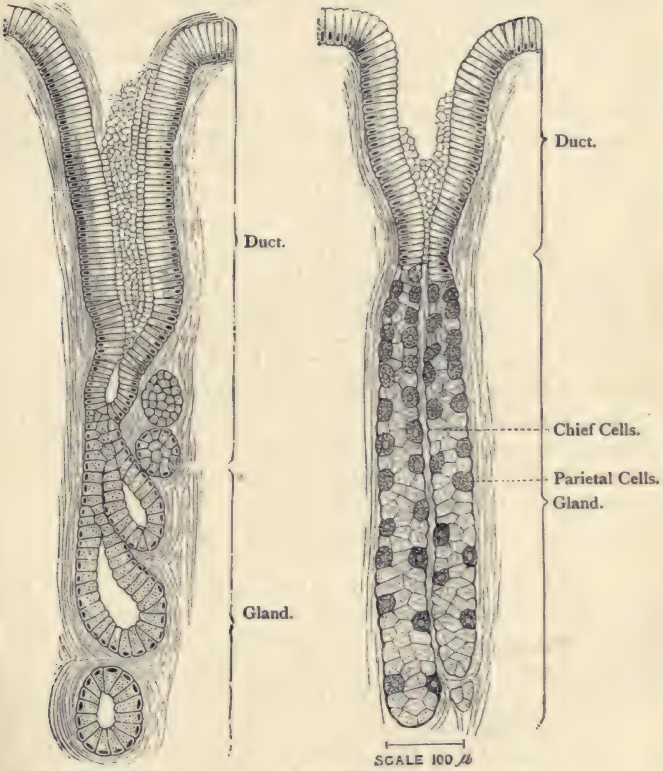
The following are Ellenberger's views on the nature of the stomach acids: In the contents of the stomach, hydrochloric, lactic, butyric, and acetic acids may be found, the two latter in insignificant quantities only. In flesh-feeders HCl predominates, 0·25 per cent., and lactic acid is found, in small quantities. In vegetable feeders lactic acid at first predominates, 0·4 per cent., and later HCl is present in small quantities; lactic acid exists throughout the whole stomach, but predominates in the right and left sacs, whilst hydrochloric acid principally exists in the fundus region. Lactic is the first digestive acid employed, but towards the end of a long digestion hydrochloric exists throughout the whole stomach. The amount of lactic acid found in the stomach of the horse during the first hours of digestion is considerable.

It has been suggested that the presence of lactic acid in the stomach of herbivora may be due to the fermentation of the carbohydrates of the food, and this cannot be doubted as a contributory cause. In the dog, in which animal the acid is doubtless hydrochloric, it is well known that no free HCl may be obtained for the first hour or two of digestion, owing to the acid combining with the protein of the food, and the diminution it undergoes in neutralising the alkali of the saliva.

The writer's experience regarding the presence of hydrochloric acid and organic acids in the stomach contents is that, no matter at what period of digestion observations have been made, on only two or three occasions has he succeeded in finding hydrochloric acid in the stomach of the horse, and he is convinced that lactic is the chief, if not the sole, digestive acid in this animal.

The **Secretion of Gastric Juice** is accomplished in certain glands known as the gastric. In man these are divided into cardiac and pyloric, each having not only a different structure, but a separate function. In the horse cardiac glands are impossible owing to the presence of the cuticular coat; but it has been shown that the villous coat contains glands corresponding to cardiac, which are principally situated in the greater curvature, at the fundus of the stomach, and extending over a limited area, described on p. 174 as not larger than one square foot (Fig. 62).

The two kinds of gland employed in the production of gastric juice are both found in the villous coat—the one in the fundus, the other in the pyloric portion, though Ellenberger states that he has found fundus glands in the pyloric region. They are simple or divided tubes lying side by side, and opening, generally in groups, on the surface of the mucous membrane by means of a shallow depression in the coat. These depressions can readily be seen studded over the tunic of the fundus, giving it a rough appearance owing to the elevation of the mucous membrane between the openings of the glands; in the pyloric region the membrane is as smooth as that found in the intestine. Each gland consists of a body, neck, and mouth, and is lined with cells; it is in respect of the cellular contents that the pyloric and fundus glands differ.



PYLORIC GLAND. CARDIAC OR FUNDUS GLAND.

FIG. 67.—THE GASTRIC GLANDS AFTER HEIDENHAIN (WALLER).

The cells of the **fundus gland** (Fig. 67) are small, polyhedral, granular, and nucleated, and line the lumen of the gland; they are called the *principal*, *central*, or *chief cells*. Scattered amongst the principal cells, but existing in larger numbers at the neck of the gland than at its base, are found certain large cells (oval, granular, and nucleated), which from their position relative to the lumen of the gland are called *parietal*, *marginal*, or *border cells*. These cells are distinctive of the fundus glands, and they stain readily with aniline blue.

The **pyloric gland** (Fig. 67) below its neck has but one variety of cell—viz., the cylindrical—containing a nucleus at its attached edge. The duct is lined, above the neck, by the ordinary epithelium of the stomach, and the same remark applies to the fundus glands; it is from this epithelium that the mucus is secreted. The important distinction between the fundus gland with its principal and parietal cells, and the pyloric gland with only its principal cells, is that the former secretes both the pepsin and acid of the gastric juice (the acid being separated from the blood by the parietal cells), whilst the pepsin only is formed by the principal cells. The pyloric glands, on the contrary, only secrete pepsin and no acid.

We have previously mentioned that the cells of the salivary glands undergo certain changes in appearance, the result of rest and activity; the same remark applies to the gastric follicles, in which the general type of changes during secretory activity is very closely allied to those already described. Langley has found that in the active state the granules decrease in number, the cells becoming clear, and capable of differentiation into a clear outer and a granular inner zone, just as we have seen in the parotid gland; during rest the entire cell becomes granular. The parietal cells during digestion were found to increase in size, but did not characteristically lose their granules. The central cells secrete both the pepsin and rennin ferments, but in neither case do these exist as such in the cells, but as a mother substance or *zymogen* of the ferments. The formation by the parietal cells of a free acid from the alkaline blood is a special chemical change, the result of selective powers possessed by the cells. In those animals, such as the dog, yielding hydrochloric acid, the cells very possibly form it by an interaction of the sodium chloride and sodium dihydrogen phosphate of the blood; but, as a matter of fact, no explanation of how the neutral chlorides are broken up with the formation of hydrochloric acid is at present satisfactory.

Mucin is secreted by mucous glands found in the deep layers of the villous membrane, especially in the region of the fundus; the epithelial cells lining the excretory ducts of the gastric glands also take part in the process. The amount of mucin formed in the stomach of the horse is remarkable ; it adheres to the villous coat like unboiled white of egg, and cannot be washed away, even by a powerful jet of water. The amount secreted is unknown, but must be considerable ; less is formed during hunger than during activity, and there is less in ruminants than in horses.

Gastric Juice.—It is only lately that a pure sample of gastric juice (but not from the horse) has been available for analysis. Most of the previous secretions examined have been a mixture of saliva, gastric juice, and perhaps other substances. Pawlow devised a method by which the stomach of the dog could be rendered available for physiological inquiry, and a pure secretion was obtained (see Figs. 68 and 69).

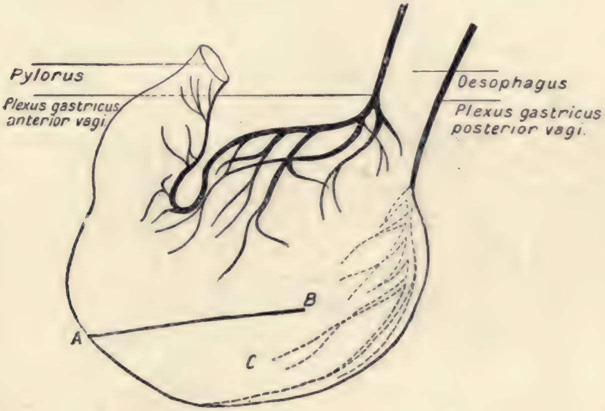

Pylorus
Plexus gastricus anterior vagi
Oesophagus
Plexus gastricus posterior vagi.
B
A
C

Fig. 68.—Pawlow's Stomach Pouch.

A, *B*, Line of incision ; *C*, flap for forming the stomach pouch. At the base of the flap the serous and muscular coats are preserved, and only the mucous membrane divided, so that the branches of the vagus going to the pouch are not severed.

Pure gastric juice in the dog is as colourless as water, and possesses a specific gravity of 1002 to 1004 ; it is thin—that is to say, is not mucinous—and of a strongly acid reaction. Chemically it consists of acid and enzymes ; it contains 0·4277 per cent. of dried material, of which 0·1325 is ash. The latter contains 24 per cent. potassium, 19 per cent. sodium, and 0·18 per cent. calcium. The acid, which is hydrochloric, amounts to 0·46 to 0·56 per cent., gastric juice being the only secretion in the body containing a free acid. Pawlow states that the total chlorine contents of the secretion are twice that found in blood, and that he has obtained 5 grammes chlorine from the secretion in 3¼ hours—an amount equal to that in the entire blood. There are two, perhaps three, enzymes present in the juice—viz., pepsin, rennin, and possibly lipase : the former is unable to act, excepting in an acid medium, and furnishes the only example in the body of this necessary combination. Exclusive of the ferments, protein is present. How far the gastric juice of other animals resembles in its composition that of the dog we have no means of knowing, inasmuch as a pure secretion has not been obtained ; but in all cases an acid and an enzyme are present. The enzyme is invariably pepsin, but the acid is not always hydrochloric. The amount of juice secreted is uncertain ; in the dog some 700 c.c. (24½ ounces) have been collected in a few hours, from which we may perhaps imagine that a considerable amount is formed in the stomach of the larger animals.

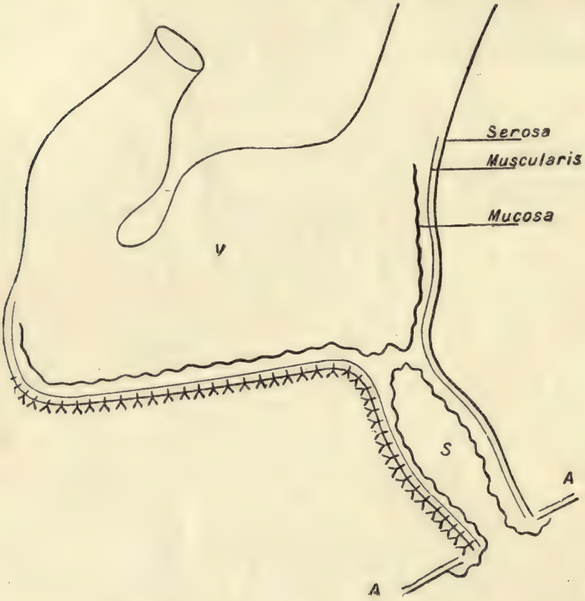


FIG. 69.—PAWLOW'S STOMACH POUCH.

S, The completed pouch ; *V*, cavity of the stomach ; *A*, *A*, the abdominal wall.

Pawlow's experiments on the dog show that the amount of juice secreted is directly proportional to the amount of food eaten : for example, 100 grammes of meat required 26 c.c. of juice, and 400 grammes needed 106 c.c. The same fact was observed on a mixed diet of meat, bread, and milk ; if these were increased by half or doubled the juice was increased in the same ratios.

The gastric juice of the dog withstands putrefaction for a long time; it may be kept for months without undergoing any important change. Not so with herbivora; the mixed gastric fluids of the horse rapidly putrefy. The antiseptic properties of the dog's juice are attributed to its hydrochloric acid; if this is so, it is additional evidence against the acid of herbivora being hydrochloric. There appears to be no reason why lactic acid should not be formed by the marginal cells of the fundus glands, but a source of lactic supply in herbivora is the carbohydrate of their food.

Pepsin is of a protein nature, though very little is known of it chemically. It exhibits its action best at a temperature of the interior of the body (37° to 40° C.); a low temperature retards its activity, while it is destroyed at a high one. The ordinary commercial product is very impure; it is an extract of the mucous membrane of the stomach, to which starch or milk sugar has been added. In physiological work a glycerin extract of the mucous membrane of the stomach suffices, to which is added some dilute HCl. Glycerin has the power of extracting the ferments both from the stomach and other portions of the digestive tract, such as the pancreas. The pepsin is formed, as we have seen, in the chief cells of the gastric glands as a zymogen or *propepsin*, which becomes pepsin after secretion. The action of pepsin is almost wholly, if not entirely, confined to the protein constituents of food. It converts the insoluble proteins into soluble ones, not by direct transformation, but by several stages. The products intermediate between protein and peptone have received certain names suggestive of differences in their chemical nature, but as to all of this a good deal of doubt and speculation exists.

In the following table the various stages of conversion are indicated in the order in which they are found to occur as determined by small differences in the chemical tests, such as solubility or colour reaction, yielded by the peptonised product. The table is the one drawn up by Kühne:

1. *The protein as consumed, or native albumin.*
2. *Acid albumin or syntonin.*
3. *Primary proteoses.*
4. *Secondary proteoses.*
5. *Peptones.*

The protein, having reached the stage of peptones, is now capable of being absorbed, but the conversion from protein to peptone is a most complex one, during which the large protein molecule is converted into simpler products of an infinitely smaller molecular weight, while so great is the complexity that the resulting product, peptone, is in all probability a group of compounds, rather than a single one, which only resemble each other in their solubility and their definite reaction to certain chemical tests. There is good reason for thinking that peptone may not even represent the final end-product in the stomach, but that still simpler bodies, to which the name **peptoids** has been given, may be formed.

Rennin is the second enzyme found in the gastric juice; it is produced in the chief cells of the gastric glands as a *prorennin*, and is subsequently, on secretion, changed into rennin under the influence of the acid present. The enzyme can be readily obtained from the true stomach of the calf, but not from the pyloric end. Commercially, rennin is used in the manufacture of cheese, a good extract causing very rapid clotting of milk. This process closely resembles the clotting of blood, and, like it, is followed by a contraction of the clot, resulting in a solid substance known as *curds*, and a yellowish fluid, *whey*. The above process further resembles blood-clotting in requiring the presence of a calcium salt. The conversion of the casein of milk into curd is believed to involve two distinct processes: first, the formation of a substance known as *paracasein* by the action of rennin; and, secondly, the action of lime salts on paracasein, by which means the curd is produced. It is even considered that the lime salts are of more importance than the rennin, as no clotting occurs in milk deprived of its calcium salts. The curdling of milk brought about by the lactic acid organism may be familiarly recognised when milk 'turns sour'; it is not the same as clotting, but represents the precipitation of casein by an acid.

There would appear to be no necessity for animals to possess this ferment after weaning, as milk does not form an article of diet for animals, if we except the chemically altered milk given to the pig. Once the curd is formed in digestion, the process is carried on by pepsin, rennin taking no further part.

Rennin has been described as existing in the pancreas, testis, and in vegetable tissues, but little is definitely known. It is stated that an *antirennin* may be formed in the blood by immunising an animal by injections of rennin, and that the substance produced prevents milk clotting.

Other ferment actions of the gastric juice have been described, such as fat- and starch-splitting. A fat-splitting ferment, allied to pancreatic lipase, may, it is said, be extracted from the gastric mucous membrane of young animals, but of the existence of this ferment there is very little evidence. Protein digestion is the essential duty of the stomach, while in all vegetable feeders maceration of the vegetable fibres is begun in the stomach as a preliminary measure. A stomach is not essential to life in all animals; in the dog, for example, it may be removed experimentally, for, as we shall see later on, protein digestion is provided for elsewhere. But in the herbivora, especially ruminants, a stomach is essential. The chief value of the stomach in those animals which can be proved to live without it lies in the preparation of the food for subsequent digestion in the small intestines, for it is quite undoubted that protein previously acted upon by gastric juice is far more thoroughly handled by the pancreatic fluid than protein not so previously acted upon.

Influence of the Nervous System on the Secretion of Gastric Juice.—By means of Pawlow's fistula, it has been proved that the secretion of gastric juice is under the control of the nervous system, the secretory fibres being contained in the vagus. Stimulation of the peripheral end of the divided nerve causes secretion after a slight delay; the cause of the latent period is unknown. No secretion results in consequence of mechanical stimulation of the stomach wall, which is contrary to all previously accepted views. The sight of food, its smell, taste, mastication, and swallowing, are direct excitants of secretion. A secretion so obtained is known as psychical. Pawlow's experiment of 'sham feeding' a dog with a divided œsophagus, the upper end of which is brought outside, has placed this beyond doubt. The animal indulged in a meal which never entered the stomach, but the effect of which could be ascertained through the fistula. In addition to this reflex secretion, there is another produced by the action of the food substances themselves; such substances, known as **secretagogues,** directly stimulate the production of gastric juice, though all foods do not possess this power. Bread, starch, fat, and white of eggs, introduced surreptitiously into a Pawlow's fistula so that the animal does not see them, do not excite secretion; while, on the contrary, meat extract is most effective.

Secretagogues may also influence the production of gastric juice through the products of digestion. This **chemical secretion** is difficult to explain; it occurs after the vagus and all other nervous connections are cut, which suggests that it does not operate through a nervous reflex. It has been shown by Edkins that the injection into the blood of an extract of pyloric mucous membrane, specially prepared, causes a marked secretion of gastric juice, and it is suggested that the chemical secretion above referred to may be produced by the action of the secretagogues upon the pyloric mucous membrane, resulting in the formation of a *gastric secretion,* or *gastrin,* analogous to *pancreatic secretion* (yet to be studied), which, when absorbed into the blood, acts as a chemical excitant, and stimulates the production of gastric juice.

Pawlow believes that the quantity and quality of the gastric juice will be found to depend on the character of the food, so that while in some cases an economical production is obtained, in others a stronger or weaker fluid is poured out, depending upon the work to be done, the regulation of which is probably a specific action on the part of the food itself.

In a meal of meat, bread, and milk, taken separately, each article of diet produces not only a definite rate of secretion of gastric juice, but also an alteration in the quality of the ferment suited to the work it has to perform. Thus flesh or bread cause a maximum secretion during the first hour of digestion ; milk during the second or third hour. The greatest digestive powers of the gastric juice are found to occur with a meat diet, while the weakest proteolytic action occurs with milk.

If an animal fed for weeks on a bread-and-milk diet be suddenly placed on meat, the power of dealing with protein is at first weak ; the juice is in sympathy with a starchy rather than a protein diet. If another change be made when the meat diet is being satisfactorily dealt with, and the animal put back on bread and milk, the whole process has to be reversed, and the glands this time brought into tune with a starchy rather than a protein diet.

It is true this observation has been made on the pancreatic juice, but what holds true for it cannot be doubted as being true for other digestive secretions. Further, we have the overwhelming proof of everyday management of horses that sudden changes in diet are productive of disease. Whether the above facts regarding digestive juices and changes in diet are explained by what we know of the function of chemical excitants—‘ *hormones* ’ —remains to be proved.

Such is the modern aspect of stomach digestion. We appear to have approached appreciably nearer to a better understanding of the circumstances attendihg digestive troubles in the horse, and, as we shall have to point out again in dealing with pancreatic secretion, Pawlow's work explains why a sudden change of a long-continued diet is bad, and as we know, is followed in horses by disastrous consequences.

Starch Conversion.—There are other changes occurring in the stomach independently of peptonising or of gastric juice. If a horse be fed on oats and the stomach fluid examined, it will be found to contain an abundance of sugar. The sugar is produced from the starch of the grain, and is not, according to our observations, the result of the action of saliva. Abundant saliva exists in the stomach, but it will be remembered that in the horse we have never succeeded in getting it to give any evidence of starch conversion. The question, therefore, is, What is the cause of this formation of sugar? It has been shown that oats may yield a starch-converting ferment, and the view that the grain provides its own enzyme for the conversion of starch into sugar may be provisionally accepted as the explanation of the presence of sugar in the stomach of the horse. The whole of the starch is not thus converted, for distinct evidence of unaltered starch can be obtained in the first portion of the small intestines. Further, some of the starch is no doubt converted into lactic acid, and the presence of this acid in the proportion of 2 per cent. does not in any way inhibit the amylolytic action. If oats provide their own starch-converting enzyme, we see the strongest argument against boiled food for horses—a practice we believe to be deleterious, or even dangerous.

Fats are not acted upon in the stomach, though the envelope surrounding the fat globule is digested, and the fat set free.

Cellulose fermentation is considered by Tappeiner to occur in the left sac of the stomach, and when marsh-gas has been found in this organ, it results from cellulose decomposition. Brown* has shown that the destruction of the cell wall of oats and barley occurs in the stomach, where it is dissolved by a cyto-hydrolytic ferment *pre-existent in the grain*; the changes occur with extraordinary rapidity in the stomach of the horse. The researches of this observer on a cellulose-dissolving ferment are of the greatest interest to the veterinary physiologist, and of considerable practical importance.

Periods of Stomach Digestion in the Horse.—Stomach digestion in the horse has been divided by Ellenberger and Hofmeister into certain periods corresponding to definite chemical changes in the food. For example, it is said that during the two first periods, which between them last two and three hours, starch conversion, lactic acid fermentation, and proteid conversion to a limited extent occur. In the third period mixed digestion of starch and protein occurs, while in the fourth and last period only protein digestion takes place. The third and fourth periods may together last four hours and upwards. We must be careful to avoid regarding these periods as based on some rigid law; they are very variable in duration, due to causes we have previously considered, and run imperceptibly into each other. With this caution we give the following periods at which gastric digestion is said by Ellenberger and Hofmeister to be at its maximum in the horse:

After a moderate feed digestion is at its height in 3 or 4 hours.
,, full ,, ,, ,, ,, 6 to 8 ,,
,, an immoderate ,, delayed still longer.

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* 'On the Search for a Cellulose-dissolving Enzyme,' H. T. Brown, F.R.S., *Journal of the Chemical Society*, 1892, p. 352.

Stomach Digestion in Ruminants.

The **Rumen** is divided into four sacs, by the constrictions produced in its wall by large muscular bands, which on the interior of the organ are of immense thickness, and well deserve the name of pillars. The interior of the organ is lined with a well-developed mucous membrane, covered with pointed papillæ, 3 to 9 mm. in length, excepting where the muscular pillars are most prominent. A few small glands are described as existing in this mucous membrane, but they form no digestive secretion. The rumen communicates freely with the reticulum; by means of the œsophageal groove it is connected with the omasum, and it naturally connects with the œsophagus. Material in the rumen can do one of three things—either pass into the reticulum, into the omasum, or into the œsophagus. The way to the omasum is via the œsophageal groove.

The **Œsophageal Groove** or gutter is a canal with an incomplete wall, which runs from the entrance of the œsophagus to the omasum. On its way it has growing from it two diverticula with which it communicates—viz., the rumen and reticulum—and it is in order to connect it with these that the wall of the canal is incomplete. This groove from the œsophagus to the omasum runs on the inner wall of the reticulum, but at no time is the interior of the canal itself visible, as it is provided with two lips—thin above, thick and crossing below—which lie in such careless yet complete apposition as to hide the groove until the lips are separated.

The capacity of the rumen is enormous: 100 litres (22 gallons) can be stored in it in the ox; 4 to 6 litres (8¾ gallons) in the sheep. Its muscular bands are arranged in two diameter-like girdles, and their function is very obviously to contract on the contents. All solid food, on being received from the mouth, enters the rumen; all fluid substances may enter any or all of the four compartments—viz., they may proceed to the abomasum direct, as is the case in the calf, or they may go to the rumen or reticulum, as most fluids—viz., saliva and the water consumed—do in the adult. Colin assured himself, with his hand in the stomach, through a window in the abdominal wall, that during the first mastication very little passes to the third and fourth compartments, and that little is fluid. Without fluid the rumen can do no work; cut off the supply, and rumination ceases. This explains the necessity of the enormous salivary secretion in these animals. The rule appears to be that the bulk of the fluid arriving in the stomach is divided between the first and second compartments, the overflow from these passing into the third and fourth sacs.

As food arrives in the rumen it passes into what Colin has described as the lower story, a part which never empties itself, and consists of the usual coarse ingesta and fluid. As the stomach fills, the mass extends into the upper story, the stomach dilating, and finally the reservoir becomes full to the roof, though not tightly packed. The last arrival in the rumen is naturally received in the anterior extremity of the left sac, and from here it passes through all hemispheres of the rumen. Material from the posterior part of the rumen makes its way forwards towards the œsophageal opening for remastication, and there can be no doubt that the mass in these sacs is actually revolved; for material capable of identification, if introduced into the stomach through a wound in the abdominal wall, gradually disappears, and returns to the same place in from twelve to twenty-four hours.

Colin, through the window in the abdominal wall, was able, by illumination, to inspect the interior during digestion, and while food was still arriving in the compartment. He observed that the level of the mass varied from moment to moment, rising and falling alternately; he could even see a portion rise up out of the mass, detach itself, and pass backwards. At other times the detached portion moved forwards; in either case it disappeared into the body of the organ, and was churned up again later on. During rumination or when fluids are swallowed this oscillation of the mass is most energetic, and, as Colin expresses it, the flow and return flow are most interesting to witness. They induce the most complete mixing of the contents, that which was at the top passing to the bottom, while the material at the bottom passes to the top. Evidence of the complete nature of the churning movements of the rumen is afforded by the perfectly spherical ' hair balls ' which are sometimes found there. Stimulation of the mucous membrane of the rumen provokes contraction of the walls, especially of the muscular pillars.

The contents of the rumen are alkaline generally, more markedly in the lower than in the upper parts, where, in fact, a slightly acid reaction may be obtained from food fermentation. Very frequently the nature of the reaction is doubtful. The alkaline reaction is due to the saliva, for there is no secretion from the wall of the rumen.

The essential function of the rumen is to retain the food for remastication, to macerate all fibrous substances and to fit them for cellulose digestion, which here takes place possibly under the influence of ferments contained in the food itself. The amount of cellulose digested in the rumen has been estimated at between 60 and 70 per cent. The result of the decomposition of cellulose is the production of a considerable quantity of gas. Ellenberger is of opinion that, in addition to the functions named, other digestive changes occur; he says that carbohydrates are digested by means of enzymes contained in the food, and in this way starch and cane sugar are converted into maltose. Proteins are also slowly converted into peptones, not through any true peptic ferment, but by some enzyme provided by the food. The rumen never empties itself; even after prolonged starvation it contains food. In young ruminants digestion occurs principally in the fourth stomach, the other compartments being rudimentary; when the young animal is placed on solid food, it is remarkable how soon these compartments develop, and the process of remastication established.

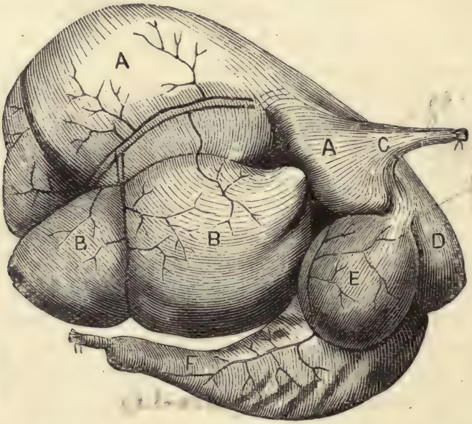

FIG. 70.—THE GASTRIC COMPARTMENTS AND TRUE STOMACH OF RUMINANTS (COLIN).

C, The œsophagus ; A, A, left hemisphere, B, B, right hemisphere of the rumen ; D, the reticulum ; E, the omasum ; F, the abomasum.

The **Reticulum,** or second gastric reservoir, is a small one placed anteriorly and inferiorly, resting, in fact, on the sternum (see Fig. 72). Its capacity in the ox is 2 litres (3½ pints), and in the sheep 0·2 litre (0·35 pint). Anteriorly it communicates with the rumen by a large opening formed by a constriction of its walls; the bulk of the organ lies below this opening. Over the lip which separates the two chambers, fluids and solids may pass in either direction. The reticulum communicates with the œsophagus, under the opening of which it is placed like a sac, while on its inner wall is the œsophageal groove, by which it communicates with the omasum. The muscular coat of the reticulum is largely striated, being a continuation of the œsophagus, and, in consequence, the movements of the compartment are not only powerful, but energetic. The mucous membrane on its interior is arranged in polyhedral cells 10 to 15 mm. in depth, closely resembling a honeycomb. In these cells stones, gravel, and foreign bodies may frequently be found, the latter frequently penetrating the heart.

The contents of this compartment are fluid and alkaline, the fluid being derived from that swallowed, and from the rumen; the alkaline reaction is due to the saliva, for, so far as we know, the mucous membrane possesses no secretory activity. The fluid in the reticulum is of use in rumination, and is forced into the œsophagus by a contraction of the walls of the viscus; it may also be forced into the rumen. Colin, with his hand in this sac, the presence of which produced energetic contractions, found the fluid poured over his hand, flooding the contents of the rumen. In order that fluid may be retained in this bag, the openings out of it are situated considerably above the base of the organ; and, further, the reticulum is so situated relatively to the rumen that it receives the overflow of fluid from that compartment when it contracts.

Ellenberger is of opinion that the reticulum regulates the passage of food from the first to the third compartment, and from the rumen to the œsophagus. In transferring the contents of the rumen to the omasum, the reticulum contracts and forces the material into the œsophageal groove. Flourens showed that the reticulum was not essential to rumination, for he excised it in a sheep, and rumination was not interfered with.

The **Omasum,** or third compartment, is quite different from those hitherto examined. Placed between the reticulum and abomasum, the viscus does its work with its contents inverted. The openings into and out of a stomach or diverticulum are generally above the portion holding the contents, but in the omasum the contents are above the openings which lead into and out of it. The omasum defies the laws of gravity.

This third compartment communicates anteriorly with the second and posteriorly with the fourth, by means of a canal three or four inches long, which runs obliquely backwards, downwards, and to the right. It is over this canal that the structure of the omasum is placed. The interior arrangement of the organ is most singular, being composed of several large leaves running the length of the organ, between these are smaller leaves, and between these a third and then a fourth series. Altogether about one hundred laminæ of variable size are found in the compartment. The leaves are papillated, the papillæ at the reticulum end being large, horny, and pointed; towards the omasum end they lose the pointed character and become warty. Ellenberger, who has specially worked out the physiology of this organ, and whose description we intend to follow, describes the anterior papillæ as resembling the teeth of a harrow, the posterior papillæ those of a file. In all cases the papillæ are arranged with their free end pointing towards the abomasum, the object of this being to direct the food towards the abomasum, and prevent its reflux towards the reticulum when the walls of the organ contract.

The food may find its way into the omasum, either directly from the œsophagus after remastication, or from the first or second compartments. It is probable that its chief source of supply is directly from the œsophagus, the omasum being drawn forwards towards it by a contraction of the pillars of the œsophageal groove, by which means communication with the rumen and reticulum is cut off. Normally the reaction of the contents of the omasum is neutral ; if found acid, it is due to regurgitation from the true stomach.

We have the authority of Ellenberger for saying that the organ secretes no digestive fluid, nor does it absorb. It is peculiar in possessing a separate source of nerve-supply, stimulation of the pneumogastric producing contraction of all the other compartments but this.

Further evidence of an independent nerve-supply is furnished by the fact that after death the walls of the other stomachs relax, but that of the omasum remains contracted.

When the food arrives at the omasum the opening leading to the abomasum is closed, and by means of the horny papillæ at the reticulum end of the organ the material is divided and directed towards the leaves, the œsophageal groove at the same time closing in order to prevent a reflux. The presence of the food then causes a reflex contraction of the leaves, by which they are rendered rigid and tense, and advance to meet the mass. The leaves having been drawn forward, the fibres now relax, by which movement the food is carried back with them. The direction of the papillæ on the leaves prevents the material from falling out of the chambers formed between the leaves, while the curve of the organ enables the leaves to give each other mutual support, like the bricks in an arch, so that no muscular effort is required to maintain the food in position. The walls of the omasum are strong, the circular fibres being three or four times as thick and powerful as those longitudinally placed ; contraction of the walls is almost constantly occurring. In this way the contents of the omasum are moved towards the fourth stomach, the position and direction of the papillæ preventing them from travelling in the other direction. Each contraction drives the ingesta not only towards the omasum, but more completely between the laminæ of the deeper system. These leaves take no part in emptying the omasum ; their function is to advance and meet the incoming matter, then to raise it to the system of channels formed by the series, and finally, by means of their papillæ, to further grind down and reduce insufficiently remasticated food. This grinding or rasping down is effected by the leaves becoming shorter, thicker, and stiffer ; the processes on them are drawn through the mass like the teeth of a harrow. The movement of the leaves is not simultaneous, but successive ; while one is passing in one direction, its fellow is travelling in the opposite direction, so that rasping of the food is continually going on, and this is evident from the fact that the contents are much finer at the abomasum end than at the reticulum end of the organ. Ellenberger, therefore, speaks of the third compartment as a triturating apparatus, a masticatory stomach, the contents of which are dry because the fluid part is being constantly strained off.

With illness rumination ceases, and the chief supply of fluid to the omasum is then cut off—viz., the saliva, which is reswallowed during rumination, and as no fresh ingesta is entering the omasum, the contents rapidly become dry and caked.

The **Abomasum** is the true digestive stomach, and is the only compartment secreting gastric juice. In the abomasum proteins are converted into peptones, the region of the cardia being in this respect more active than the pylorus. Ellenberger states that starch is also digested, and that this precedes protein digestion. In the fourth stomach of the calf a milk-curdling ferment (rennin) exists, which has already been dealt with.

Stomach Digestion in the Pig.

The stomach of the pig is peculiar ; it is a type between the carnivorous and ruminant, and is divided by Ellenberger and Hofmeister into five distinct regions, which do not all possess the same digestive activity.

The gastric juice of the pig contains for the first hour or two of digestion lactic, and afterwards hydrochloric, acid ; pepsin is present, and, it is said, a ferment which converts starch into sugar. In the pig, according to the above observers, the process of digestion is not the same in all regions of the viscus ; one may contain hydrochloric acid, another lactic ; one may be abundant in sugar, while this may be absent elsewhere. The first stage of digestion is one of starch conversion ; the second is the same, only more pronounced ; the third stage is one of starch and protein conversion, both processes occurring at the cardia, but only protein conversion taking place at the fundus ;

lactic acid is present in the former, and both lactic and hydrochloric acid in the latter. In the fourth stage starch conversion is nearly complete, while hydrochloric acid predominates in all the regions, and protein conversion is general.

Stomach Digestion in the Dog.

Very complete knowledge of the physiology of the dog's stomach exists, for nearly all the work carried out to elucidate the physiology of the human stomach has been effected on the dog, and has, to some extent, already been embodied in the previous pages in dealing with gastric juice.

In the stomach of the dog and cat digestion occurs mainly in the pyloric dilatation or antrum, which is from time to time cut off from the rest of the stomach by the pyloric ring or transverse band (not to be confused with the pyloric sphincter), so that the general body of the stomach acts mainly as a receptacle, passes, from time to time, material into the antrum for chyme conversion, and then ejects it into the intestines. The length of time material lies in the stomach depends upon its nature and consistence; both carbohydrates and fats escape into the intestines more readily than protein, and this appears to depend upon the strength of acid present. A weaker acid sufficing for non-protein food is more rapidly neutralised in the small intestines, and the opening of the pylorus appears to depend upon impulses passing from the duodenum as soon as the last received acid supply has been neutralised in that bowel.

A flesh diet requires very little saliva and practically no mastication, but its digestion is slow, in spite of the fact that it is taken in a form closely allied to that in which it is assimilated. Colin states that it takes a dog twelve hours to digest an amount of meat which it could eat at one meal. The substances most difficult of digestion are tendons and ligaments, but their digestion is facilitated by boiling; liver and flesh are best given raw, as cooking interferes with their digestibility. The gastric juice of the dog is fully described at p. 187.

Absorption from the Stomach.—The needful changes having occurred in the stomach—and we now refer principally to the stomach of the horse—the next step is to inquire into the proportion of food so altered as to be rendered fit for absorption.

Experiment shows that in the stomach 40 to 50 per cent. of the carbohydrates have been converted into sugar, whilst 40 to 70 per cent. of the proteins are converted into peptones. When food has been long in the stomach, not more than 10 per cent. of the proteins escape being peptonised. In ruminants probably the greater part of the food substance is acted upon in the gastric compartments and stomach, leaving comparatively little for the intestines to perform.

In spite of the changes which occur in the stomach, it has been proved by the experiments of Colin that *no absorption occurs from this organ in the horse.* It would be useless to recapitulate all his experiments ; they were generally performed with strychnine, and he found that, so long as the pylorus was securely tied, no symptoms of poisoning occurred when the alkaloid was introduced into the stomach, no matter how long it was left there, but that when the ligature was untied, and the contents of the stomach passed into the intestines, poisoning rapidly followed. These remarkable results were obtained by him so often, and under such varying conditions, as to leave no doubt as to the accuracy of the observations. Strychnine experiments are not altogether free from objection, but as matters stand we can only surmise that no absorption of sugar or peptones occurs in the stomach. It is certainly very remarkable what becomes of the peptones ; the writer has never found any in the stomach contents, no matter at what period of digestion the examination was made, and if they are not absorbed in the stomach they must pass very rapidly into the intestines and enter the vessels at once, as no peptone can be found in the small intestines. Colin attributes the absence of absorption from the stomach of the horse to the small area of the mucous membrane, which, he says, cannot be secreting gastric juice and absorbing at the same time. In the empty stomach he attributes the non-absorption of poisons to the thick layer of tenacious mucus which, as we have previously mentioned, covers the villous stomach of the horse. Colin's experiments also show that there is little or no absorption from the abomasum of ruminants. On the other hand, there is absorption from the stomach of the dog and pig. Recent experiments on the dog show that absorption does not take place readily from the stomach. Water taken alone is practically not absorbed at all ; sugars and peptones are absorbed only when in sufficient concentration, while fats are not absorbed.

Self-Digestion of the Stomach.—A question which for a long time gave rise to an energetic discussion was the reason why the stomach during life does not digest itself, seeing that the action of its secretion is so potent that portions of living material, legs of frogs, ears of rabbits, etc., if introduced into it, are readily digested, also that post-mortem digestion of the stomach in some animals is far from rare. The walls of the stomach are not singular in possessing a specific resistance to a digestive fluid. The small intestine is immune to trypsin, which, if injected under the skin, digests the tissues and produces ulceration. Fæces and urine are very irritating, excepting, so to speak, in their own home. The bladder never shows any sign of irritation from the presence of urine, but if it be paralysed, and the urine, in dribbling away, falls on the skin, the part in time ulcerates, and very early becomes excoriated. Even tears running over the face, in cases of obstruction of the duct, cause the skin to ulcerate. In spite of the action of gastric juice, ' bots ' live in the stomach for months, and, unfortunately, are never digested. Parasites of the digestive tract enjoy the same immunity from digestion that the membrane of the canal possesses.

It is now generally believed that the immunity enjoyed by the tissues in contact with active or irritating secretions is due to the local formation of an antibody. That in the stomach has been named *antipepsin*, and its function is to neutralise the digestive action of the gastric juice on the living wall.

We have never yet met with post-mortem digestion of the stomach in the horse ; whether this be due to the horse's acid being mainly or wholly lactic cannot be definitely stated.

The Gases of the Stomach.—The nature of these largely depends upon the food—for example, green food is most productive of gas, owing to the active fermentation it undergoes. Traces of oxygen, a quantity of carbonic acid, and variable amounts of marsh-gas, sulphuretted hydrogen, hydrogen, and nitrogen, are found. The oxygen and nitrogen are derived from the swallowed air, the carbonic acid is derived from the fermentation of the food and the action of acids on the saliva, while the marsh-gas is obtained by the decomposition of cellulose.

The gases from the intestines of the horse and rumen of the ox are very commonly inflammable, and burn with a pale blue flame. This is due to marsh-gas, which may be readily ignited when mixed with a due proportion of oxygen.

Vomiting and Rumination.

Vomiting amongst solipeds and ruminants is rare, but the act is common in the dog and pig.

The reasons given as to why the horse does not *ordinarily* vomit are various : (1) The thickened and contracted cardiac extremity of the œsophagus ; (2) the oblique manner in which the latter enters the gastric walls ; (3) the dilated pylorus lying close to the contracted cardia, so that compression of the stomach contents forces them into the duodenum ; (4) the cuticular coat thrown into folds over the opening of the cardia ;

(5) muscular loops encircling the cardia, the contraction of which keeps the opening tightly closed; (6) the stomach not being in contact with the abdominal wall. All these and other reasons have been assigned as the cause of non-vomiting in the horse. Yet on turning to ruminants, which also normally do not vomit, we find the stomach, gastric compartments, and œsophagus freely communicating, the largest reservoir lying in contact with the abdominal wall, the cardia freely open, the œsophagus of great size, and, still stranger, the animal possessing the ability, under the control of the will, to bring up food from the stomach as a normal condition, and yet unable to vomit! It is evident, therefore, that all these theories are not sufficiently satisfactory to account for the absence of vomiting, and we are bound to suppose that the vomiting centres in the medulla of both horse and ox are either only rudimentary or very insensitive to ordinary impressions.

Vomition in the horse is no doubt seriously interfered with by the thickened œsophagus, contracted cardia, and the arrangement of the muscular fibres. The folds of mucous membrane filling up the orifice could offer no serious obstruction to a distended stomach, for it is known that even when this membrane is dissected away post mortem, a stomach will burst rather than allow fluid or air pumped in at the pylorus to escape at the cardia, unless the muscular fibres surrounding it be partly divided. Vomition in the horse is generally indicative of ruptured stomach, and much has been written as to whether vomiting occurs before or after rupture. From no inconsiderable experience of these cases, the writer has arrived at the conclusion that it may occur at either time, and that a horse may vomit though a rent 7 or 8 inches long exists in the stomach wall.

Dilatation of the cardia and œsophagus is essential to the act of vomition in the horse, and in all cases where vomiting occurs during life the cardia is so dilated that two or three fingers may readily be introduced into it. It is perfectly possible for a horse to vomit and recover (showing that it had not a ruptured stomach), and it is not unusual to have attempts at or actual vomition when the small or large intestines are twisted. Vomiting in the horse is not as a rule attended by any distressing symptoms; the ingesta dribble away from one or both nostrils; occasionally an effort is made on the part of the patient, the head being depressed to facilitate expulsion, but more than this is very rarely seen.*

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* The only case of vomiting the writer has seen in the horse which resembled that presented by the human subject was in a case of volvulus of the small bowels. The horse was lying on his chest with the nose extended, the ingesta gushed in a stream from both nostrils, and a sound accompanied the effort.

It is important to notice in connection with the subject of vomiting that agents such as tartar emetic, ipecacuanha, and apomorphia, which excite vomiting by their action on the cerebral centre, have no effect on the horse or ruminants, nor does the horse vomit as the result of sea-sickness, though he suffers extremely from it. Why he should vomit more often with a ruptured stomach than a sound one is a fact we cannot explain.

In those animals where vomiting is a natural process, the three important factors are—The dilatation of the cardia by active contraction of the longitudinal fibres of the œsophagus, pressure on the walls of the stomach by a contraction of the diaphragm and abdominal muscles, and closure of the pylorus. But there is some evidence to show that the stomach itself is not passive ; it is true Majendie produced vomiting after he had replaced the stomach by a bladder, but under normal conditions there appears no reason why the stomach wall should remain quiescent, and in the cat it has been observed that during vomiting a strong contraction of the pyloric end of the stomach occurred, shutting it off from the cardiac portion. We may here have one explanation of ruptured stomach in the horse, which supports the view put forward on p. 176 of the influence of the duodenal trap.

Rumination.—The physiology of rumination has been principally worked out in France by Flourens and Colin, and our knowledge of this singular process is based almost entirely on their observations.

The œsophagus in ruminants has its inner layer of fibres spirally arranged in double obliquity; the tube is wider at its termination than in the part which precedes it. On entering the gastric reservoirs, it forms a groove, previously described (p. 194), which brings it into connection with all the sacs comprising the stomach. In this way material coming down the œsophagus may enter either or any of the reservoirs, the choice being determined by the condition in which it is swallowed.

The lips or pillars of the œsophageal groove are composed of involuntary muscular fibres, arranged longitudinally and transversely (Fig. 71), by which means the groove can be shortened and constricted. By a contraction of the pillars, the omasum may be drawn forward and brought nearly in apposition with the œsophagus. By relaxation of the pillars the œsophagus is made to communicate with either the first or second reservoir. Fig. 72 shows the rumen and reticulum in position. The œsophageal groove is represented as open, though normally its lips cover it so perfectly that it requires looking for. The close proximity of the reticulum to the heart will be observed, and in this connection see the remarks on p. 197. At one time it was considered that the œsophageal groove took an important share in rumination, but the question was decided by Colin in his usual thorough manner by stitching the pillars together, and it was found this did not interfere with the process. Prior to this experiment it was believed that the lips formed the bolus, and then passed it into the œsophagus. Colin, with his hand in the stomach, introduced ingesta into the canal, but could not succeed in getting the lips to grasp and carry it into the œsophagus. Additional evidence is furnished by the llama, which ruminates and has but one pillar to the groove.

During the churning movements of the stomach the material is being gradually pressed forwards in the direction of the œsophagus and against the lips of the groove, ready for regurgitation. This latter is effected by the diaphragm being fixed in its inspiratory position, and the simultaneous contraction of the walls of the rumen, reticulum, and abdomen. By these means some of their contents is forced into the œsophagus, fluid from the reticulum, and semi-solid from the rumen. In the œsophagus the bolus is cut off by the cardiac end of the tube, and by reversed peristaltic action the bolus is conveyed to the mouth, the soft palate being raised and cutting off the posterior nares. In passing under the velum the liquid portion is squeezed out, and is at once reswallowed, passing to the third compartment, while the solid material is ground. If the left abdominal wall be auscultated during rumination, certain sounds may be heard. One of these Colin describes as resembling a crepitant lung râle, and is due to the disengagement of gas in the rumen; another is a friction sound resembling that heard in pleurisy, due to the gliding motion of the gastric reservoirs against the abdominal wall and diaphragm; and a third sound is heard at the moment the fluid returns from the mouth. Gurgling sounds may also be heard over the œsophagus in the neck at the moment of swallowing.

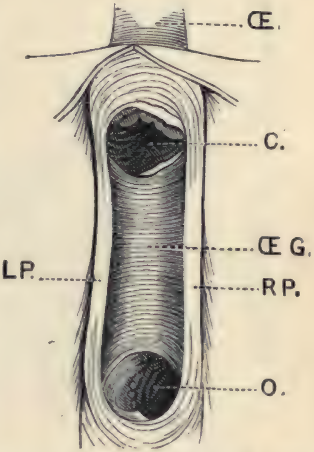

FIG. 71.—DIAGRAM OF THE ŒSOPHAGEAL GROOVE, WITH THE MUCOUS MEMBRANE STRIPPED OFF TO SHOW ITS MUSCULAR FIBRES (CARPENTER).

Œ, Œsophagus entering the stomach; C, its cardiac opening; RP, right pillar of œsophageal groove; LP, left pillar of the same; O, opening into the omasum; ŒG, œsophageal groove extending from C to O, about 7 inches in length.

The bolus in the mouth may weigh from 100 to 120 grammes (3 to 4 ounces), and it is projected into this cavity with such force that if the mouth is open it may drop out. Its remastication occupies about fifty seconds; it is then reswallowed, and passes to the third compartment, or, if not sufficiently comminuted, it returns to the rumen, and is once more remasticated.

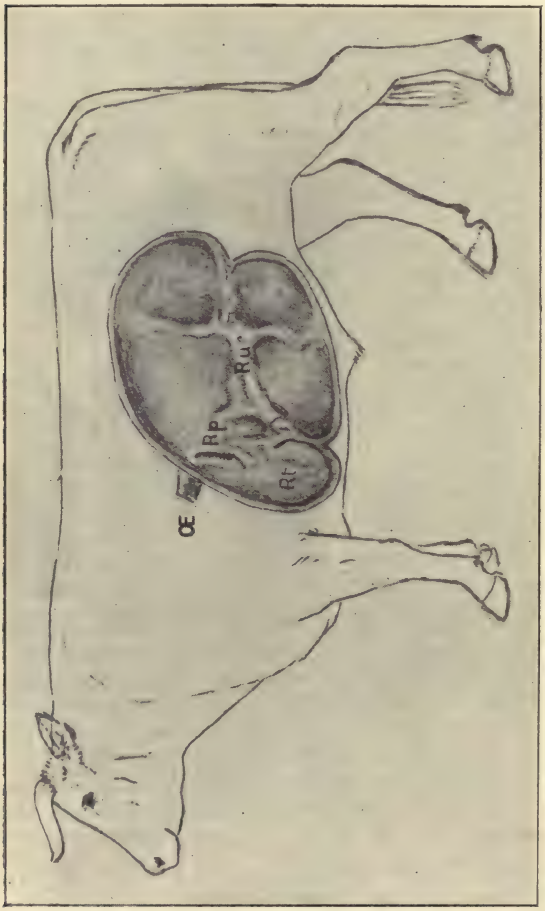

Fig. 72.—The Position of the Œsophageal Groove in the Living Animal.

Ru, Rumen: the lettering is placed on the muscular pillars. Rt, reticulum. Œ, œsophagus. Rp, right pillar of œsophageal groove: both pillars are represented as if held apart in order to show the canal.

The ascent and descent of the bolus in the neck may be readily seen, and Colin has estimated that each of these requires 1·5 seconds, while an equal period is required for the formation of a fresh bolus. On this data, from the time the bolus is prepared until its return must occupy 54·5 seconds. One minute might be taken as sufficiently near. Rumination is, therefore, a slow process, and occupies at least seven hours out of the twenty-four. It is remarkable the length of time an animal will continue to ruminate while using the jaws in one direction; from the effort involved frequent changes of direction might have appeared to be necessary, but such is not the case. One-quarter to half an hour's mastication on one side may be performed.

The animal prefers a recumbent position for the process, but draught oxen may be seen ruminating in the yoke, and camels while carrying their burden.

The share taken by the reticulum is mainly the supply of fluid to the mass, but rumination can occur even after the removal of the reticulum. A certain distension of the rumen is absolutely necessary; though this organ never empties itself, it must contain a fair amount of food before rumination begins; further, it must contain a considerable quantity of fluid. If the salivary flow which so largely contributes to this fluid be diverted, remastication becomes difficult, though for a day or two rumination may be carried on; later it begins to fail, and it is only by a great effort of the abdominal muscles that food can be passed into the œsophagus. Colin's experiment in this direction showed that by the thirteenth day rumination was no longer possible. It has been shown that the parotids of the ruminant are always in a state of activity, and the object of this continuous secretion is to insure the function of rumination being duly carried out.

An animal alarmed or disturbed at once ceases to ruminate, and one of the earliest signs of ill-health is that the function is suspended.

Rumination is a reflex nervous act, the centre for which probably lies in the medulla. The act can only be performed by means of the united action of the diaphragm, walls of the stomach, and abdominal muscles. Hence, if the phrenics be divided, rumination is carried out with great difficulty, and only by an extra effort of the abdominal muscles; if the vagi be divided, the walls of the stomach are paralysed, and the process cannot go on; if the spinal cord be divided in the mid-dorsal region, the abdominal walls are paralysed, and rumination can no longer occur.

Movements of Food in the Stomach.

A good deal of exact information as to the manner in which the stomach behaves in dealing with its contents has been obtained by means of direct experimental inquiry. Colin, in the case of the ruminant, introduced his arm into the organ through an external opening. In the horse, carefully conducted feeding experiments have helped to show what is occurring from hour to hour, but it was not until the aid of X rays was taken advantage of that the process could be seen occurring in the intact living animal.

If a cat be fed on a diet liberally mixed with bismuth, the process of digestion can be watched by X rays, owing to bismuth being opaque to these rays. Within a few minutes of the entry of food into the stomach, contractions, which begin at the middle of the organ and end of the pylorus, are started. As digestion advances the contractions become stronger and regular, occurring at intervals of about ten seconds, and travelling to the pylorus, which is reached in twenty seconds. Periodically the pylorus is relaxed, and chyme forcibly propelled into the duodenum ; after every discharge it closes, and in course of time the process is repeated. All idea of a churning motion occurring in simple stomachs has now been abandoned ; it was difficult to disprove, except in the case of the horse, until X rays were employed. In the horse the arrangement of the food in the stomach in strata as received never left any doubt that churning took no part in the process of stomach digestion in this animal. It will be observed that the cardiac end of the stomach of the cat takes apparently no share in the movement, and it is probable that in most animals the œsophageal end plays but a passive part. In the horse, in fact, it may be regarded more in the light of an œsophageal dilatation.

If the abdominal cavity be rapidly opened in a recently destroyed horse it may be possible to see the stomach at work. Its peristalsis is slow, rather more deliberate and less energetic than intestinal peristalsis, and not infrequently hour-glass constrictions may appear, though not to a marked degree. Many observations may be made before gastric peristalsis is seen ; unlike intestinal peristalsis, it is not always present after death.

The mechanism controlling the opening and closing of the pylorus is by no means clear ; solid bodies are denied a passage for some time, and even for chyme the pylorus does not open with every contraction wave which passes over the stomach. A bullet administered as a bolus was found in the stomach thirty-six hours later, though the animal had in the meantime been fed, from which it seems certain that the pylorus is capable of deciding what should and what should not pass. Yet in the case of the horse some modification in this statement must be made, for, as has been shown, owing to the small size of the stomach and the bulky nature of the food in an organ already filled, an amount passes out at one end equal to that being taken in at the other, and where this mechanism fails disease at once arises.

Probably most liquids rapidly pass out of the stomach, especially so in the horse; the bulky requirements of this animal could not be contained in the stomach, and in fact if, while an animal is drinking, auscultation be practised, water may be heard passing along the duodenum below the right kidney.

Little of what has hitherto been said applies to ruminants. The movements of their stomach wall are complex; the immense muscular pillars of the rumen are capable, as we have seen, of mixing, churning, and revolving the contents of the organ. That rotation occurs is certain from the formation of hair balls from material swallowed by the animal in licking its body, or, in the case of sheep, from wool torn out when scratching themselves, and subsequently swallowed. The rumen and omasum are constantly at work, the rumen contracting a little oftener than three times a minute; the reticulum, on the other hand, has periods of rest, likewise the true stomach. In the latter the movements must be of a most simple character, such as occurs in the single stomach of other animals.

The movements of the stomach are excited by the presence of food, or any irritation applied to the mucous membrane. These movements are rendered more energetic by stimulation of the vagus, but even when all the nerves going to the part are divided, the stomach can still contract, which is probably due to the ganglia contained in its walls. The stomach is, in fact, an automatic organ. It is supplied by both pneumogastrics, the nerves being non-medullated; in addition, it obtains sympathetic fibres from the solar plexus, to which the right vagus also sends some fibres (see Fig. 80, p. 228). In the wall of the stomach ganglia are found with which both the vagus and sympathetic communicate. The vagus may be regarded as the motor nerve of the stomach, while the sympathetic is mainly inhibitory; stimulation of the vagus leads to contraction of the stomach walls, stimulation of the sympathetic causes dilatation of a contracted stomach and relaxation of the pylorus. The vagus supplies the bloodvessels with dilator fibres, whilst the sympathetic supplies them with constrictor fibres. Section of the vagus in the horse causes paralysis of the stomach, and in other animals, if the movements are not abolished, they are certainly diminished. The result of stomach paralysis is that nothing passes on to the intestines, so that in the horse even large poisonous doses of strychnine may thus fail to cause death by lying inert in the stomach. This experiment demonstrates the uselessness of giving medicine by the mouth in many cases of digestive troubles in the horse; the material lies in the stomach owing to paralysis of the organ, and is never absorbed.

The *nervous mechanism of the stomach of ruminants* is derived mainly from the vagus, excepting for the third compartment, which has a separate and, at present, unknown source of supply. Stimulation of the vagus was found by Ellenberger to produce energetic contraction of the reticulum, slow kneading movements of the rumen, and slower and later-appearing peristaltic contractions of the abomasum, but no contraction of the omasum. Section of both vagi was found to paralyse the œsophagus, rumen, and reticulum, followed by tympany of the rumen. Ellenberger could not obtain any effect on the stomach movements by stimulating the sympathetics.

The influence of the mind over stomach digestion is well known in man, and we have already noted its effect in the experimental feeding of the horse related at p. 180. Pawlow's fistula has enabled this point in the lower animals to be settled with accuracy. One of his dogs, while actively secreting gastric juice under the influence of a 'sham meal,' was made angry and excited by being restrained from chasing a cat; the gastric glands at once ceased secreting. Similarly by means of X rays the movements of the cat's stomach have been observed to cease when the animal became angry and excited.

SECTION 3.

Intestinal Digestion.

The chyme which is poured from the stomach into the small intestines meets there with three digestive fluids—viz., the succus entericus, the bile, and the pancreatic juice.

The **Succus Entericus** is prepared by the glands of the small intestines; in the duodenum the glands of Brunner are found, while the follicles of Lieberkühn are met with throughout the whole of the small and large intestines. Lieberkühn's crypts supply a considerable proportion of intestinal juice, while the secretion from the glands of Brunner is scanty. Brunner's glands, which are very large in the horse, are arranged on the same principle as the gastric glands, while those of Lieberkühn are tubular glands, amongst the cylindrical epithelial cells of which numerous mucus-forming goblet cells may be found.

The total amount of succus entericus secreted by the horse is given by Colin as 10 litres (17 pints).

At one time it was considered that the succus entericus was a comparatively unimportant fluid, the chief function of which was to neutralise the acid chyme; Colin, however, showed that in the horse it has a distinctly digestive effect. It is now known that though a pure secretion of Lieberkühn's crypts has little or no digestive action excepting on starch, an extract of, and juice squeezed from the intestinal wall has a most important function. The Lieberkühn fluid is quantitatively small in amount, and alkaline in reaction due to carbonate of soda. The intestinal extract, on the other hand, contains three enzymes, and in addition a peculiar chemical substance of remarkable properties. The enzymes are:

1. **Enterokinase,** which converts the trypsinogen, the mother substance of the pancreatic proteolytic enzyme, into trypsin.

2. **Erepsin,** a proteolytic ferment, which supplements the work of trypsin, acting on deutero-albumoses and peptones, breaking them up into amido-acids and hexone bases.

3. **Inverting Ferments,** converting double sugars which cannot be utilised by the tissues into single sugars which can. Of inverting ferments there are three:

Maltase, converting maltose and dextrin into dextrose.

Invertase, converting cane sugar into dextrose and levulose.

Lactase, converting milk sugar into dextrose and galactose.

Finally, the intestinal fluid contains **secretin,** which is not a ferment, but a chemical substance found in the walls of the small intestines ; this when taken into the blood possesses the singular property of causing the secretion of pancreatic juice.

Enterokinase, erepsin, and secretin will be dealt with in considering the pancreas.

Intestinal Digestion in the Horse.

The contents of the stomach are neutralised by the pancreatic and biliary secretions immediately or shortly after they leave the stomach. So much is this the case that on the duodenal side of the pylorus the reaction of previously acid chyme is neutral, and a few inches along the duodenum it is alkaline ; this alkaline reaction is at first faint, but becomes more marked as the ileum is approached. Ellenberger describes the contents of the small intestines as being acid in the first two-thirds of their length, then neutral as far as the ileum, where they become alkaline ; we have only once found them otherwise than alkaline throughout. He further states that in the fasting horse the contents are alkaline, but that in the digesting animal, whether horse, ox, or sheep, they are acid, the acidity decreasing after passing the common duct, and becoming decidedly alkaline at the posterior portion of the small intestine. This, as we have said, does not agree with the writer's experience in the horse ; it is usual to find the contents of the duodenum next the pylorus neutral, and from this point the bowel is faintly alkaline, the reaction increasing in intensity up to the ileum, where the contents are always markedly alkaline. We have only once found the small bowels acid in the horse, no matter what diet has been given, or at what period of digestion the examination has been made ; a neutral or faintly alkaline reaction in the anterior part of their course, and marked alkalinity in the posterior portion, is doubtless the rule rather than the exception.

The arrangement of the small intestines suspended or dangling in festoons from the spine through the medium of a very delicate membrane is a construction the advantages of which are not very apparent. It appears to invite trouble. The long mesentery is considered to favour volvulus, but no doubt the chief cause of this latter trouble is tympany. If the bowels be artificially distended with air, loops of them behave in such a way as would lead to twist in the living animal.

Physical Characters of the Chyme.—The chyme having passed into the bowel, its appearance at once changes, for the acid albumin is precipitated by the alkaline secretion found there. It is now observed that the material consists of clots floating or suspended in a yellowish fluid, extremely slimy in nature, and resembling in appearance, through its precipitated albumin, nasal mucus suspended in fluid. The proportion of mucin must be considerable, judging from its ropiness when poured from one vessel to another, and this mucus is probably largely derived from the stomach. Throughout the small intestines the character of the chyme is as follows—viz., a yellow, frothy, precipitated, slimy fluid, the material from the anterior part of the intestinal canal having a peculiar mawkish smell, while that from the region of the ileum is of a distinctly fæcal odour ; the latter is due to indol and skatol formed putrefactively during pancreatic digestion. In the ileum the proportion of fluid material is considerably reduced in amount, and the character of the ingesta may now be recognised, which was previously almost impossible.

Function of the Ileum.—As the flow of material into the small intestines is controlled by a sphincter, so is the flow out of them. The ileum is a remarkably thick and powerful bowel ; it is always found contracted and containing material which is dry compared with that found in the anterior portion of the intestine. One of the functions of the ileum is to control the passage of material into the cæcum. Colin describes the chyme in the horse as circulating between the pylorus and ileum—viz., that it is poured backwards and forwards in order to expose it sufficiently to the absorbent surface ; this necessitates a reversed peristaltic action. He says that were it not for this the material could not be acted upon and absorbed, as the passage of fluid through the small intestines is very rapid. It would have been impossible to reason out that the fluid material of the small intestines was passed to and fro between the stomach and the ileum, exposed, as Colin expresses it, twenty times over to the absorbent surface of the bowels. This observation must have been made as the result of his examination of the living animal, and there can be no doubt of its correctness.

Experiment shows that water will pass from the stomach to the cæcum in from five to fifteen minutes. By applying the ear over the duodenum, as it passes under the last rib on the right side, the water which a horse at that moment is drinking may be heard rushing through the intestines on its way to the cæcum. One is always struck by the fact that the small intestines are never seen full—in fact, are often practically empty—from which we judge either that material passes very rapidly through them, or that only small amounts of chyme are propelled into them at a time. The contents are always in a liquid condition excepting at the ileum, the fluid being derived from the secretions poured into and those originating in the bowel. That active absorption goes on in the intestines is proved by the difference in the physical characters of the contents in their several parts. The rate at which the chyme passes through the small intestines varies with the nature of the food, and the frequency with which the horse is fed. Ellenberger says it reaches the cæcum six hours after feeding, but has not entirely passed into this bowel for twelve or even twenty hours ; we have known it reach the cæcum in four hours.

In the small intestines the chyme meets with the bile and pancreatic juice ; the action of these on food will be described in the chapter dealing with the liver and pancreas. The absorption of chyle, and its elaboration before reaching the blood, are points which must be reserved for the chapter on ' Absorption.'

Large Intestines.

There can be no doubt that in solipeds digestion in the large intestines is a very important process ; at least, we judge so from the fact of their enormous development. In many respects they present a considerable contrast to the small intestines ; for instance, they are always found filled with ingesta, the contents are more solid, the material lies a considerable time in them, and there are no juices other than the succus entericus poured into the bowel. These are conditions exactly the reverse of those found in the small intestines. The bowels which are spoken of as the large intestines are the cæcum, double and single colon, and the rectum.

The **Cæcum** has been described by Ellenberger as a second stomach ; its enormous capacity and fantastic shape have always rendered it an intestine of considerable interest (Fig. 73). To our mind its most remarkable feature is that it is a bag, the openings into and out of which are both found at the upper part close together ; the exit, strange to say, is above the inlet, and the contents have to work against gravity in order to obtain an entry into the next intestine, the double colon. This is brought about by the four muscular bands on the cæcum (Fig. 74), which shorten the bowel, forcing the contents upwards towards the ' crook.' The ileum being closed, the only available outlet is into the colon (Fig. 75).

Several questions suggest themselves regarding the communication between the large and small intestines. It is certain that in order to get from the ileum into the colon everything must pass into or, at any rate, through the cæcum, yet we feel sure that material does not remain there long. Is it possible that the openings of the ileum and colon might be brought together so that material may pass directly from one into the other ? Nothing is returned into the ileum from the cæcum ; there must be, in consequence, a sphincter keeping the ileum closed, for when the cæcum contracts material must cross the opening of the ileum in order to reach the colon (Fig. 75). This sphincter is furnished by the thickened condition of the wall of the ileum. We see no difficulty in believing that the rigid end of this tube

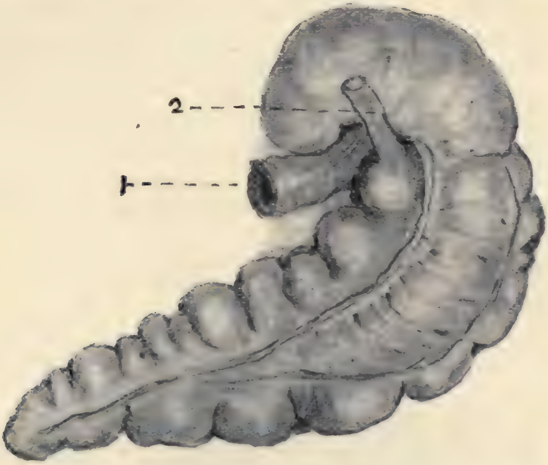

FIG. 73.—CÆCUM OF THE HORSE IN POSITION, ITS INNER FACE BEING SEEN.

1, The first colon; 2, the ileum.

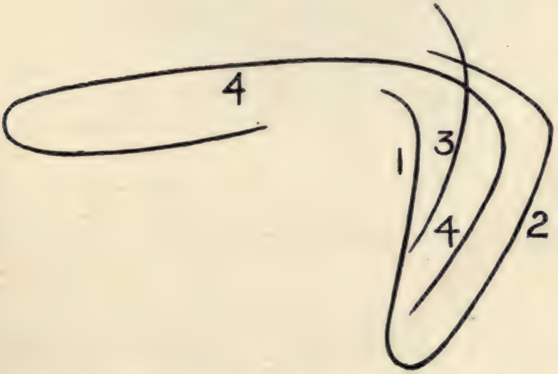

FIG. 74.—SCHEMATIC ARRANGEMENT OF THE LONGITUDINAL MUSCULAR BANDS OF THE CÆCUM.

Bands 1 and 2 are one, and form a complete sling for the bowel; band 4 runs from the cæcum to the pelvic flexure of the colon. It is a remarkable band, and doubtless intimately connected with the mechanism which brings about the passage of material from cæcum to colon.

may pass its contents practically direct into the colon, and the slightly funnel-shaped arrangement of the latter would readily admit the rigid nozzle of the ileum.

The contents of the cæcum are always fluid, sometimes quite watery, occasionally of the colour and consistence of pea-soup, in which condition they are full of gas bubbles ; when watery, the fluid is generally brownish in colour, with particles of ingesta floating about in it. The reaction of the contents is always alkaline ; all observers are agreed on this point.*

The cæcum is most admirably arranged as a receptacle for fluids, and though absorption undoubtedly occurs from it, and digestion of cellulose takes place in it, yet we believe its chief function is the storing up of water for the wants of the body and the digestive requirements, as it is absolutely certain that digestion in the horse can only be properly carried out when the contents are kept in a fairly fluid condition. We do not say that the cæcum produces no digestive changes in the food, for we have stated that the contents are occasionally of the consistence of pea-soup, but we consider its digestive function subordinate to its water-holding one. Ellenberger views the cæcum as a bowel for the digestion of cellulose, where by churning, maceration, and decomposition, this substance is dissolved and rendered fit for

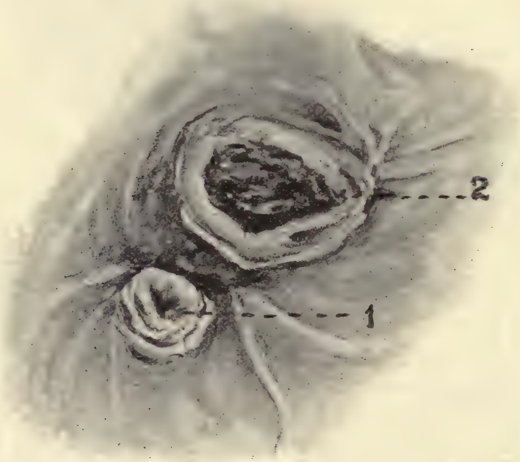

Fig. 75.—The Opening of the Ileum and Colon in the Cæcum.

1, The ileum ; 2, the colon. In the figure the openings are represented close together, but even when stretched apart they are less than 4 inches distant.

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* The writer only once found the cæcum acid.

absorption, and he likens it to the stomach of ruminants and the crop of birds. He further considers that the cæcum exists owing to the small size of the stomach, and the rapidity with which the contents are sent along the small intestines. His experiments demonstrated that the entire ‘ feed ’ reaches the cæcum between twelve and twenty-four hours after entering the stomach, that it remains there twenty-four hours, and during that time 10 to 30 per cent. of the cellulose disappears.

The digestion of cellulose is no doubt a very important matter, especially as we know that the poorer the food the more cellulose digested ; but we are not prepared to admit that food necessarily remains in the cæcum twenty-four hours, and we believe that cellulose digestion occurs principally, though not entirely, in the colon, and, further, that it is not absolutely necessary for the material to remain in the cæcum, but that it may pass on at once to the colon. The writer's experiments on digestion have shown that ingesta may reach the cæcum three to four hours after entering the mouth, and we are quite clear on the point that oats may travel some considerable distance along the colon in four hours from the time of being consumed, though this is regarded as exceptionally rapid. For example, a horse which had never had maize and had not tasted oats for two or three years, was fed first with 2½ pounds of maize, and seventeen hours later with 4 pounds of oats. The animal was destroyed four hours from the time of commencing to eat the oats. Much maize and a few oats were found in the pelvic flexure of the colon, and a certain proportion of maize and a quantity of oats in the stomach. In twenty-one hours the small ration of 2½ pounds of maize was distributed between the stomach and pelvic flexure of the colon, which is a very large area. In four hours the oats reached the same point in the bowel that the maize had arrived at ; this is exceptionally rapid, but this experiment supports two points it is desired to emphasise—viz., the difficulty in getting the stomach to empty itself completely, and the rapid transit of material through the small intestines.

Colin believed that in the cæcum starch can be converted into sugar, fats emulsified, and the active absorption of assimilable matters occur.

The Colon.—The direction taken by the colon of the horse is remarkable. It commences high up under the spine on the right side, its origin being very narrow, but it immediately becomes of immense size ; it descends towards the sternum, and, curving to the left side, rests on the ensiform cartilage and inferior abdominal wall. The colon now ascends towards the pelvis, and here makes a curve, the bowel becoming very narrow in calibre : the pelvic flexure having been formed, the intestine retraces its steps towards its starting point. Running on top of the previously described portion it descends towards the diaphragm, growing gradually larger in calibre, and then ascends towards the loin, being here of immense volume—in fact, at its largest diameter; it then suddenly contracts, and forms the single colon (see Figs. 76 and 77). The object of the difference in the volume of the double colon appears to be for the convenience of its accommodation in the abdominal cavity.

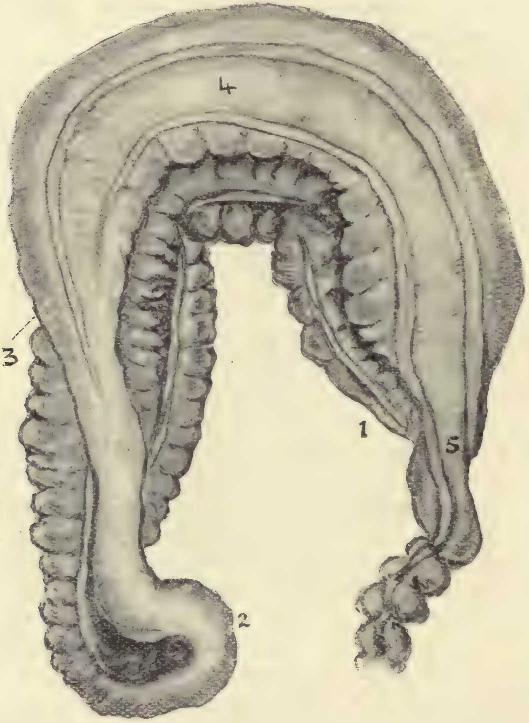

Fig. 76.—The Double Colon looked at from Above modified from Müller).

1, The first colon, the cæcum being removed; 2, the pelvic flexure, the bowel being narrow; 3, the colon suddenly enlarges; 4, its diaphragmatic flexure; 5, the single colon. Several of the bands are seen; note also the sacculated and non-sacculated portions of the bowels.

The double colon may, for the purpose of description, be divided into four portions: the ingesta in the first and third descend, in the second and fourth ascend. It is found that the physical characters of the contents are not the same throughout. In the *first colon* the food is fairly firm, and the particles of corn, etc., can be readily recognised; in the *second colon* the material is becoming more fluid, while at the *pelvic flexure* the contents are invariably in a liquid, pea-soup-like condition, and the particles of which they are composed are not readily recognised. In the *third colon* the material becomes firmer, but only slightly so, and bubbles of gas are being constantly given off from its surface; in the *fourth colon* the entire ingesta are like thick soup, and the material composing them is in a finely comminuted condition, the surface being covered with gas bubbles. For the first foot or so of the *single colon* this condition is maintained, when quite suddenly the contents are found solid and formed into balls. The remarkable suddenness of this change is invariable in a state of health, and indicates either most active absorption, or

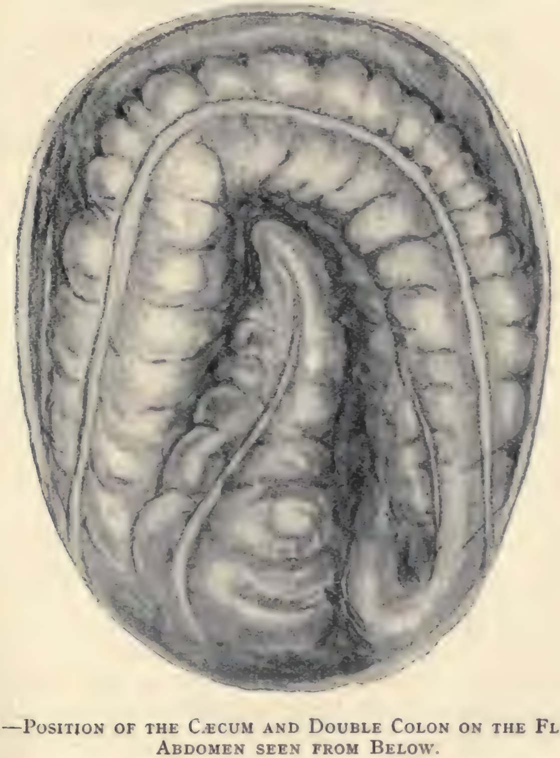

FIG. 77.—POSITION OF THE CÆCUM AND DOUBLE COLON ON THE FLOOR OF THE ABDOMEN SEEN FROM BELOW.

The point of the cæcum is directed towards the sternum. The abdomen has spread open in front owing to the needful dissection. It should be egg-shaped, the narrow end foremost.

that the contents are subjected to great compression. The entire contents of the colon are yellow in colour or yellowish-green, becoming rapidly brown or olive-green on exposure to the air; the colour being due to the chlorophyll of the food. The contents of the colon are normally alkaline throughout; we once, however, found them acid.

Digestive Changes.—Large Intestines.

The changes food undergoes in the large intestine have never excited the same interest as those in the small. The absence of any secretion from the large bowel other than the succus may help to account for this, and may also assist in explaining why the large bowels have been regarded in the light of reservoirs for ingesta, rather than as active centres of digestion. As a matter of fact, the large intestines of the horse are actively employed in dealing with cellulose, not by means of any known enzyme peculiar to the body, but rather by the process of bacterial disintegration, the result of decomposition. It is known that bacteria may hydrolyse cellulose, and render it fit for absorption. In the case of oats, we mentioned (p. 193) that they probably furnished their own cellulose enzyme, but this has not been proved for all vegetable material. The cellulose of hay is, probably, only utilised after prolonged maceration in the large intestines and the subsequent attack of bacteria. By some it has been considered that the epithelial cells of the intestine are capable of dealing with cellulose, but on this point no definite statement can be made. Cellulose yields energy to the body on oxidation, but there is another reason for the extensive preparations made for its digestion in herbivora—viz., the cellulose encloses the protein, starch, and fat of vegetable substances in a framework, and until this is broken down these substances cannot be acted upon. We know that considerable cellulose solution must occur before the material arrives at the large intestines, otherwise neither in the stomach nor small intestine could digestion occupy the prominent position it does. The digestion of protein, fat, and sugar are largely, though not entirely, dealt with in the stomach and small intestine, but there must be a certain amount of these substances so firmly locked up in their cellulose envelope that they are not liberated until after prolonged maceration and digestion in the large intestines. We may, therefore, safely assume that protein, fat, starch, and cellulose are capable of being acted upon and absorbed from the large intestines of the horse.

As the result of cellulose digestion carbonic acid and marsh-gas are formed in equal volumes. We have in our description of the large intestines drawn attention to the appearance of the cæcum and fourth portion of the double colon, with their pea-soup-like contents, on the surface of which gas bubbles are constantly breaking. It may well be that these two places are the active seats of the final transformation of cellulose, the cæcum dealing with that which has already been acted upon in the stomach and small intestines, and the fourth colon being concerned with the more refractory cellulose, which has required prolonged maceration in the large intestines before becoming capable of solution. This is rather supported by the remarkably rapid change in the character of the contents in the single colon, the pea-soup-like condition giving way, in the space of a few inches, to the appearance presented by ordinary normal fæces.

The large intestines cannot exist entirely for the solution of cellulose. There are other processes going on, chief of which is the bacterial attack on the unabsorbed protein products of the small intestines. The small intestine may be regarded as free from putrefactive processes; in fact, it is only towards the ileum that the unpleasant products of pancreatic digestion can be detected. In the large intestine, on the other hand, putrefactive processes are evident throughout; the bacteria are here engaged, among other things, in attacking the unabsorbed products of protein digestion, and reducing them to simpler end-products, such as proteoses, peptones, amido-acids, indol, skatol, phenol, phenyl-propionic, phenyl-acetic and fatty acids, with the evolution of CO_2, H_2, H_2S, and CH_4. These end-products are got rid of either through the fæces, or they are absorbed into the blood, taken to the kidneys, and, combining with sulphuric acid, are got rid of through the urine; especially is this the case with phenol, indol, and skatol.

Metschnikoff has made a special study of the organisms living in the intestinal canal of man, and has arrived at the conclusion that in the myriad population of the intestinal tract there are at least three anaerobic organisms which can produce very virulent poisons. These poisons, which are of the aromatic series, phenols and indols, are absorbed by the intestinal wall. Metschnikoff regards the colon with grave suspicion, and believes that it is the cause of men not dying from old age. It certainly cuts short the useful life of many horses.

As the material moves towards the rectum it becomes drier and drier, and more thoroughly formed into balls by the action of the bowel-sacs, which squeeze the mass into a round or oval shape. The contents of this portion are still alkaline, or slightly so. As we approach the anus a distinctly acid reaction is obtained on the surface of the fæces, though at this time the interior of the ball may be, and often is, alkaline; the converse of this may also be observed. In the rectum the single balls collect in masses, to be forced out of the body at the next evacuation. The reaction of this mass is acid, and the colour depends on the food, being, on an ordinary diet, of rather a reddish-yellow or brownish tint, due to altered chlorophyll.

Absorption from the single colon and rectum is rapid; the marked change in the physical character of the fæces is evidence of this. Animals may also be killed by the rectal injection of strychnine; narcosis can be produced by the rectal administration of ether, and life may be supported, at any rate for a short time, by means of nutrient enemata.

Intestinal Digestion in Ruminants.

Though intestinal digestion is so important in the horse, it would appear in ruminants to occupy a subordinate position. It is curious why in one animal the changes should occur at the anterior, and in the other at the posterior part of the digestive tract, but this difference in the arrangement for digesting cellulose depends upon one being capable of rumination and the other not. The rumen of the ox corresponds to the large intestines of the horse. The intestines of the ox are of extreme length, but small in calibre; they are half as long again as those of the horse, and it would appear that their chief function is that of absorption. Their arrangement, especially that of the large intestine, is most singular. The small intestines are hung in convolutions on a mesentery; they are narrow in diameter, and about 120 feet in length. The large intestines are about 9 metres (30 feet) in length, also narrow and without muscular bands or puckerings, as in the horse; the colon is arranged in a remarkable spiral manner between the folds of the mesentery (see Fig. 78). It is in this immense length of absorbent surface that the food substances capable of being utilised are taken up. It is clear, however, that certain digestive changes occur in the small intestines, into which, as in other animals, the pancreatic and biliary fluids are poured. Here the proteins which have escaped the stomach, and the fats and starches, are rapidly changed and rendered fit for assimilation; the altered cellulose in all probability only finds its way here when fit for absorption after its digestion in the rumen.

Intestinal Digestion in other Animals.

In the pig intestinal digestion is said to be of short duration, and absorption very rapid. **In the dog** the material passes out of the stomach slowly, and only in small quantities, into the small intestines, which are usually found collapsed. It is in the small intestines of this animal that the chief digestion occurs, as the large bowels are rudimentary. In the sheep, ox, pig, and dog, the reaction of the contents of the small intestines is acid anteriorly and alkaline towards the ileum; probably in all animals the contents of the large intestines are alkaline in reaction.

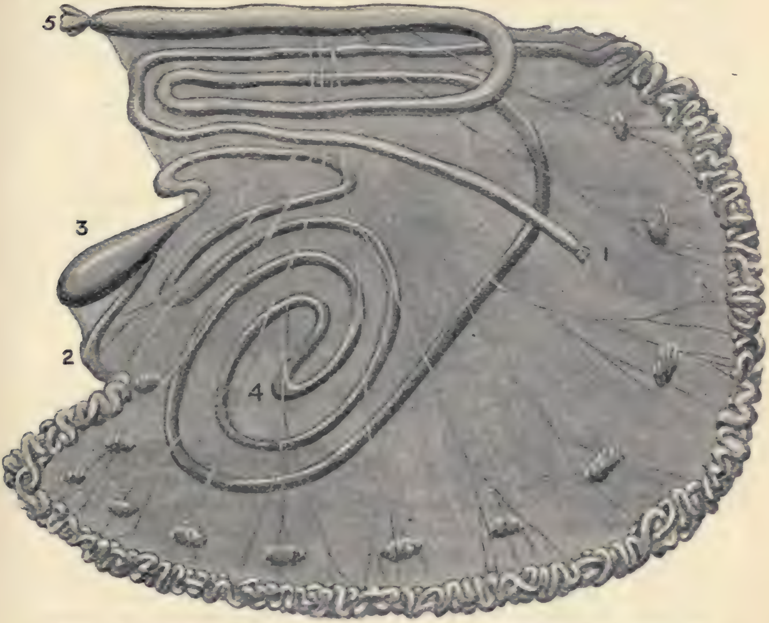

FIG. 78.—SCHEMATIC ARRANGEMENT OF THE INTESTINES OF THE OX.

1, The small intestines ; 2, their termination in the cæcum ; 3, the cæcum ; 4, the 'spiral' colon ; 5, the single colon. In the spiral colon it will be observed that the ingesta is apparently travelling in opposite directinos.

The following table gives some information regarding the intestinal canal of the domestic animals, which helps to explain some of the differences in their mode of digestion.

The intestinal capacity is, on an average :—

Horse	200 litres	—44 gallons
Ox	80 ,,	17·5 ,,
Pig	27 ,,	5·9 ,,
Dog	8 ,,	1·75 ,,

Ratio of length of intestine to length of body :

Sheep	26 times longer
Ox	20 ,, ,,
Horse	12 ,, ,,
Dog	5 ,, ,,

Movements of the Intestines.

The movements of the intestines are brought about by the involuntary muscle composing its wall. This muscle in the small intestines is arranged in two sheets in a circular and longitudinal manner, while in the large intestines narrow bands of pale muscle of considerable length take the place of the ordinary longitudinal layer, and may be found on all parts where the tube is sacculated. In fact, one function of the bands is to bring about the sacculated condition of the canal, an important arrangement whereby economy of space is effected with no loss of surface.

The sacculated condition of the double colon is confined principally to the first, second, and fourth portions. The third portion, especially at the pelvic flexure, is free from sacculations, and the fourth portion is not so liberally puckered as the first and second. On the first colon there are four bands, on the second colon there are also four, three of which disappear at the pelvic flexure; on the third portion there is only one band, while on the fourth colon there are three (see Figs. 74 and 79). In the large intestines the longitudinal layer of fibres is confined to the muscular bands, so that the great bulk of the wall consists of circular muscle only. The longitudinal bands shorten the bowel, but the main work in pressing the contents along is performed by the circular layer. The bands, in fact, are numerous where the intestine is large, and reduced in number where the bowel becomes smaller. This arrangement suggests that they may, under suitable conditions, produce an irregularity of pull, and we can see no other explanation of displacement of the large intestines of the horse (a matter dealt with more fully at the end of this chapter) than through the medium of these muscular bands.

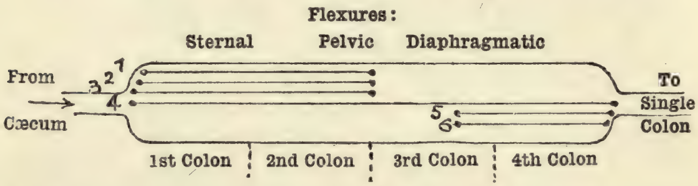

FIG. 79.—SCHEMATIC ARRANGEMENT OF THE MUSCULAR BANDS ON THE DOUBLE COLON.

The colon is supposed to be opened out into a straight tube. Bands 1, 2, and 3 run from the first colon to the pelvic flexure; one of the three actually comes from the apex of the cæcum. No. 4 is the only band running the whole length of the bowel. Nos. 5 and 6 originate in the region of the third colon, and finally run on to the single colon.

The muscular movements of the large intestine are slower than those of the small bowels; possibly one reason for this may be that the food has to remain a longer time in contact with the absorbing surface—viz., for at least forty-eight hours, and for as long as four days. The peristaltic movement of the small intestines is quite distinct from that of the large; the one ends at the ileum, the other begins at the cæcum.

The muscle of the intestinal wall causes the movement known as **peristalsis,** which normally passes in the direction stomach to rectum. Relatively quick in the small intestines, it becomes slower and more deliberate in the large, but the wave has always the one object in view—viz., to press the ingesta onward. A wave of contraction passing the reverse way—viz., in the direction of rectum to stomach—is known as **antiperistaltic**: such a movement is considered abnormal, but in the horse, according to the observations of Colin, antiperistalsis of the small intestines is a natural condition. Some physiologists recognise antiperistaltic movements of the large intestines as being normal in certain animals, producing a to-and-fro movement of the contents, but it is generally thought that in the small bowels antiperistalsis is only present under abnormal circumstances. If antiperistalsis be admitted for the large bowels, we see no difficulty in extending it to the small, especially in view of Colin's positive statement that it occurs. The peristaltic wave depends upon a something peculiar to the bowel wall, for if a piece of small intestine be experimentally reversed, so that the portion originally nearest the stomach is made to occupy a position farthest away from it, it is found that the peristaltic wave in the reversed segment is still in the original direction instead of in the new direction. The actual mechanism involved in a peristaltic contraction, according to Starling and Bayliss, is as follows: The circular muscle on the stomach side of the bolus contracts, while that on the far side is relaxed for some distance, so that the advancing wave drives the bolus into a relaxed portion of bowel. If a solution of cocaine or nicotine be applied to the intestinal wall these movements cease, from which it is argued that they are probably due to local ganglia.

Rhythmical or **Pendular** movements of the small intestines were first described by Starling and Bayliss. They consist of a series of local contractions caused by the presence of food in the canal, and occur in the dog at the rate of about twelve a minute, and in the cat thirty times a minute. They have been studied by means of the Röntgen rays and a bismuth diet. Pendular movements are essentially connected with the division and subdivision of food in the intestinal canal; by means of the rays a string of material may be seen to become suddenly segmented, each segment again dividing, and each of these again in a perfectly definite manner may be further subdivided. In this condition it is exposed to thorough mixing with the secretions in the intestine, and to enable the finely divided contents to be so acted upon the bowel at the time is free from peristalsis. When acted upon, a peristalsis sweeps together all the scattered atoms, and forms them once more into a string of material. This remarkable movement is unaffected by the action of cocaine or nicotine, which have been shown to inhibit at once the ordinary peristaltic movements.

Besides peristaltic and pendular movements, another has been described in the dog much slower, but also rhythmical, which may be carried out for twenty or thirty minutes at intervals of two hours, even when the canal is empty.

We have been told by Colin that digestion in the small intestines of the horse is carried on by peristalsis and antiperistalsis, the fluid travelling from stomach to ileum, and from the ileum towards the stomach. Pendular movements are of no value in the small intestine of this animal, as the entire material, until the ileum is reached, is fluid, so that there are no strings of food to be segmented. This may account for pendular movements of the bowels not having been observed in the horse.

In the first and third portions of the colon of the horse the ingesta travel by their own gravity ; in the second and fourth portions they travel against gravity, as in the cæcum. As the first and fourth and second and third portions of the colon are united, the curious results follow that material is passing along each section apparently in two opposite directions.

The frequency of intestinal affections in the horse causes the canal to be of exceptional practical interest. When the cæcum is found completely inverted into the colon, as if a hand had passed through the colo-cæcal opening, laid hold of the apex of the cæcum, and drawn the entire bowel within the first portion of the colon, it is then that the question of muscular movements so strongly presents itself. Or, again, what is far commoner and equally fatal—viz., displacement or actual twist of the large bowel; or a complete twist of the small intestine, leaving the bowels in such indescribable complexity that the parts cannot be unravelled, even when removed from the body! Finally, a condition rare in the horse, probably in all animals, but still well recognised, in which telescoping of the small bowels occurs, known as 'intussusception.' It is impossible to believe that muscular action of the intestines is free from all blame in the production of these lesions. It is easier to understand a twist of the small intestine apart from muscular action than it is to understand displacement or actual twist of the large intestine.

A loop or coil of small intestine may be so distended by gas or ingesta as to become twisted, but it is more difficult to imagine either of these conditions producing twist or displacement of the large intestines, and it becomes a question, as we have previously said, how far the action of the muscular bands of the bowel may have a contributing influence. That great force is necessary is undoubted, bearing in mind the difficulty, if not impossibility, of restoring the parts to their position post mortem, or endeavouring after death to reproduce the lesions experimentally. These matters will be referred to again.

Nervous Mechanism of the Intestinal Canal.—Two distinct impulses are conveyed by the intestinal nerves—viz., those for contraction and for inhibition. In the anterior part of the tract the former function is mainly or entirely carried out by the vagus, stimulation of which is found to cause active contraction of the small intestines. Contraction of the large intestines is effected through branches of nerves which issue from the sacral portion of the cord, and pass with the nervi erigentes to the hypogastric plexus. From this plexus fibres run in the coats of the large intestines, producing on stimulation much the same results as the vagus—viz., active contraction of both circular and longitudinal coats.

Stimulation of certain branches of the sympathetic nerve stops or inhibits the contractions produced by stimulation of the vagus, hence the term 'inhibitory.' The inhibitory nerves of the small intestine are derived from the dorso-lumbar portion of the cord, pass by the rami communicantes (*rc.*, Fig. 80) to the main sympathetic chain, *Sy.*, and thence through the large and small splanchnic nerves to the solar plexus, from which the final distribution to the intestines is made. The inhibitory fibres for the large intestines are derived mainly from the lumbar cord through *rc.* and *Sy.* (Fig. 80) to the inferior mesenteric ganglion. From this ganglion inhibitory fibres are supplied to both longitudinal and circular coats. The connections of the abdominal sympathetic ganglia of the horse are shown in Fig. 81.

Contractions of the bowels and peristalsis can occur after all nerves leading to the intestines have been divided ; this points to the existence of local ganglia, and such may be found in the intestinal wall. The intestinal movements are automatic and self-regulated, though they can be provoked by both chemical and mechanical stimuli. The normal stimulus to peristalsis is the passage of ingesta along the canal. In the dog even the sight of food is said to promote peristalsis. Gases, such as CO_2, H_2S, and CH_4, and organic acids, such as acetic, propionic, caprylic, etc., act as stimuli, and promote contraction, which is a fortunate

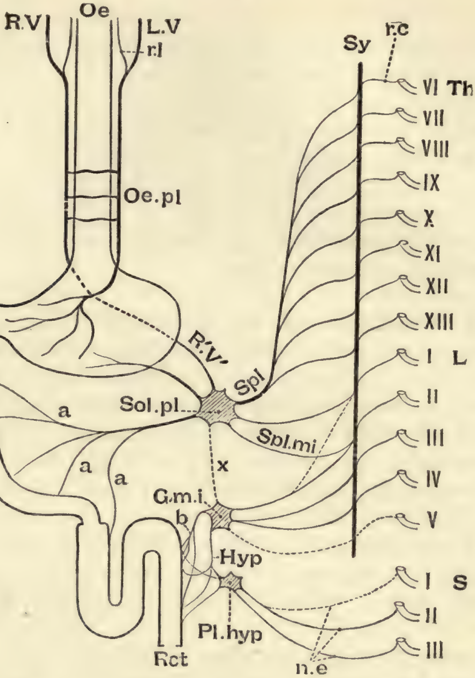

Fig. 80.—Diagram to illustrate the Nerves of the Alimentary Canal of the Dog (Foster).

(The figure is very diagrammatic, and does not represent the anatomical relations.)

Oe. to *Rct.*, The alimentary canal from the œsophagus to the rectum.

LV., Left vagus nerve ending on the front of the stomach; *r.l.*, recurrent laryngeal supplying upper part of œsophagus; *R.V.*, right vagus joining left vagus in the œsophageal plexus *Oe. pl.*, supplying the posterior part of the stomach, continued as *R′.V′.* to join the solar plexus, *Sol. pl.*, *here represented by a single ganglion*, and connected through *x* with the inferior mesenteric ganglion (or plexus). *G.m.i.* *a, a, a,* branches from the solar plexus to stomach and small intestines, and *b*, from the mesenteric ganglion to the large intestines.

Spl., Large splanchnic nerve arising from the thoracic ganglia of the sympathetic, *Sy.*, and rami communicantes, *r.c.*, of the dorsal nerves.

Spl.mi., Small splanchnic nerve. Both the large and small splanchnics join the solar plexus, and thence make their way to the alimentary canal, supplying the small intestine with inhibitory impulses.

G.m.i., Inferior mesenteric ganglion formed by nerves running from the dorsal and lumbar cord. From this ganglion inhibitory nerves are given off to the large intestines.

n.e., Nervi erigentes arising from the sacral cord, and proceeding to the hypogastric plexus. *Pl. hyp.*, from this plexus impulses of a motor kind are supplied to the large intestines.

circumstance, as they are normal to the bowel in consequence of bacterial activity. Oxygen gas, on the other hand, inhibits movements, and, as a matter of fact, we know that oxygen gas normally does not exist, or only in traces, in the gaseous contents of the bowels. Cutting off the blood-supply to the bowels causes violent contractions, which occur again when the circulation is re-established; the former is of interest in those cases of twist where the blood-supply is wholly or partly interfered with.

Under normal conditions the mind is not conscious of peristaltic movements, but when these become very energetic pain is produced. Under the influence of nervous excitement rapid and frequent evacuations of the bowels may take place in both cattle and horses. So rapid may the evacuations be that in the horse, in a short time, the whole of the rectum and single colon may be unloaded. Ordinary exercise is always an important cause of peristalsis, and of keeping the posterior bowels emptied.

As previously remarked, the normal stimulus to peristalsis is the presence of ingesta in the canal. In the feeding of herbivora bulk is essential, they cannot live in a state of health on concentrated food alone. Their intestines need bulk, if only in order to

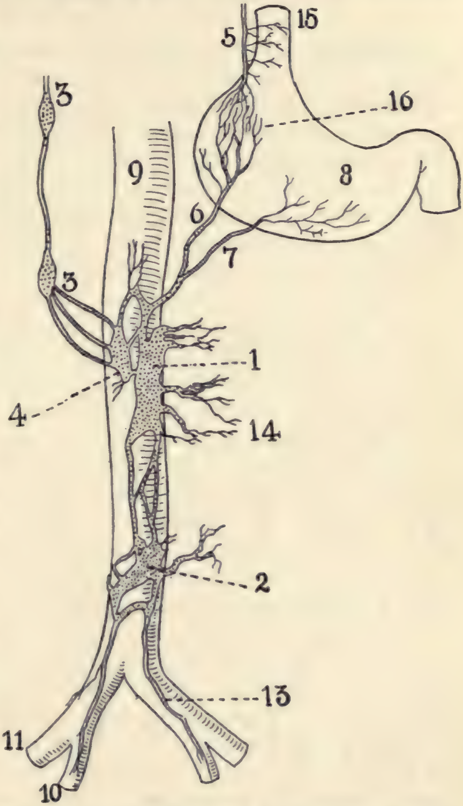

FIG. 81.—ABDOMINAL PRE-VERTEBRAL SYMPATHETIC SYSTEM OF THE HORSE.

1, Anterior mesenteric ganglion; 2, posterior mesenteric ganglion; 3, sympathetic cord under the arches of the ribs; 4, the splanchnic; 5, the vagus passing to the stomach; 6, fibres from the anterior mesenteric ganglion joining the vagus; 7, branches of the sympathetic passing to the stomach; 8, the stomach; 9, the posterior aorta; 10, the internal iliac artery; 11, the external iliac; 13, pelvic branches of sympathetic; 14, mesenteric branches of sympathetic; 15, the œsophagus; 16, rich plexus formed by vagus and sympathetic nerves.

maintain peristalsis. Bunge has shown that if cellulose be withheld from the diet of rabbits they die from intestinal obstruction. It is the cellulose and lignin in the diet of herbivora which largely provide the needful stimulus to peristalsis.

Regulation of the Digestive Processes.—Under normal conditions, excepting for hot fluids, there is no sensation in the alimentary tract posterior to the fauces ; speaking generally, once the food has passed the point mentioned, we are no longer conscious of its existence. The intestines and stomach may be handled without causing pain, though under disease when they are inflamed, tightly contracted, nipped, or immensely distended, the pain produced is acute, and, judging by the violence shown by horses, intolerable.

With the absence or apparent absence of an afferent nerve-supply, it is remarkable in what way the supreme function of the gastro-intestinal tract is kept in working order. There are no impulses passing to the brain or medulla directing operations, and it can be shown, experimentally, that extirpation of the abdominal sympathetic in the dog does not cause any interference with digestion, nor with the movements of the intestines. In fact, as we have just seen, movements of the intestines occur after all the nerves have been divided. It is more than likely that the key to the position is that furnished by Bayliss and Starling, and that the regulation of the gastro-intestinal tract is a chemical regulation by means of *hormones*. The existence of these substances has already been mentioned, and more will be said later, but it is well here to emphasize the fact that they are capable of acting after all nervous connections have been severed. They act through the medium of the blood.

Gases of the Intestines.—The largest amount of gas found in the intestinal canal is in the cæcum and colon ; the small intestines naturally contain very little, frequently none, whatever is formed there being probably rapidly passed into the large bowels. In the large intestines marsh-gas commonly exists, forming with carbonic acid the bulk of the gases present. The pathological conditions arising in the large bowels of horses, and in the rumen of cattle, as the result of fermentation—particularly of green food—and the enormous size to which these animals may in consequence be distended, are matters of common clinical experience. In both horse and ox the gas may generally be ignited a short distance away from the cannula which has been passed to give relief, the marsh-gas igniting readily on meeting with the proper proportion of oxygen. The whole of the chemical changes in the intestinal canal are carried on in the absence of oxygen ; the gases which are produced depend mainly on the nature of the food, green material producing marsh-gas and carbonic acid, leguminous matters producing sulphuretted hydrogen and hydrogen.

For **Intestinal Absorption**, see p. 283.

The Fæces.—The fæces consist of that portion of the food which is indigestible, together with that part which, though digestible, has escaped absorption ; mixed with these are water, colouring substances, mucin, organic matters in great variety, inorganic salts, bile pigment, volatile fatty acids, remains of digestive fluids, organisms, etc.

The composition of the fæces depends largely on the diet. The following table from Gamgee* is only intended to give a general idea of their nature :

APPROXIMATE COMPOSITION OF THE FÆCES OF THE HORSE, COW, SHEEP, AND PIG.

	Horse.	Cow.	Sheep.	Pig.
Water - - - -	76·0	84·0	58·0	80·0
Organic matter - -	21·0	13·6	36·0	17·0
Mineral matter - - -	3·0	2·4	6·0	3·0
	100·0	100·0	100·0	100·0

Considerable differences exist amongst animals in the consistency of the fæces ; they are moderately firm in the horse, pultaceous in the ox, and hard in the sheep. These differences depend upon the amount of fluid they contain. In the pig they are human-like and very offensive ; in the dog they are soft or hard, dark or light, depending on the diet, the mineral matter of bones producing the light-coloured excreta. It is necessary to remember that the proportion of fluid in the fæces does not depend upon the amount of water which is drunk, but rather on the character of the food, the activity of intestinal peristalsis, and the energy with which absorption is carried on in the digestive canal. Succulent green food in horses produces a liquid or pultaceous motion ; other foods, such as hay and chaff, have a constipating effect, the fæces being large and firm ; excess of nitrogenous matter in the food produces extreme fœtor of the dejecta, and frequently diarrhœa, probably due to putrefactive processes. Nervous excitement frequently induces a free action of the bowels, accompanied by liquid fæces.

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* 'Our Domestic Animals in Health and Disease,' p. 253.

Fæces always float in water so long as cohesion is maintained. The colour of the fæces in the horse is yellowish or brownish red, in the ox greenish-brown; they rapidly become darker on exposure to the air. When the animal is grass-fed the fæces are green, and when a horse is fed wholly on corn they become very yellow, and like wet bran in appearance. The colour of the fæces of animals receiving hay or grass is due to altered chlorophyll. The fæces of the horse are moulded into balls in the single colon. They are always acid in reaction, the acidity probably depending upon the development of some acid from the carbohydrates of the food.

Fæces contain lignin amongst the indigestible portion of the ingesta, a proportion of cellulose, husks of grains, the downy hair found on the kernel of oats, vegetable tubes and spirals, starch and fat granules, gums, resins, chlorophyll, etc.; unabsorbed protein, carbohydrate and fatty matters; products of digestive fermentation, such as lactic, malic, butyric, succinic, acetic, and formic acids; leucine, tyrosine, indol, skatol, and phenol; biliary matters and altered bile pigment—stercobilin—which gives the colour to the dejecta in the dog, but not in herbivora; and, lastly, mineral matter in varying proportions. In the dog portions of muscle fibre, fat-cells, tendinous and fibrous tissue, are found in animals fed on flesh.

Of the *inorganic matter* silica exists in largest amounts in herbivora, then potassium and phosphates; sodium, calcium, magnesium, and sulphates, form a smaller but still important proportion. The horse excretes but little phosphoric acid by the kidneys, but considerable quantities pass with the fæces in the form of ammonio-magnesium phosphate. This salt is derived principally from the oats and bran of the food, and it frequently forms *calculi* through collecting in the colon around a pebble or nail as a nucleus, and becomes mixed with organic substances. Other intestinal calculi are formed from lime deposits in the bowel, while collections of the fine hairs from the kernels of oats become encrusted with ammonio-magnesium phosphate, and form oat-hair calculi. In the Persian wild goat and certain antelopes intestinal concretions are found known as Bezoar stones, formerly much used in medicine, and as antidotes to poison. There are two varieties of calculi, one olive-green, the other blackish-green. The first melts when heated, emits aromatic fumes, and consists chiefly of an acid allied to cholalic acid. The chief constituent of the second variety is an acid derivative of tannic acid, which indicates their origin from food substances. Stomach calculi have not been unknown in the horse, while in cattle, as the result of licking each other, 'hair balls' are common objects.

The following table by Roger gives the mineral composition of the fæces in every 100 parts of the ash :*

	Horse.	Ox.	Sheep.
Sodium chloride	0·03	0·23	0·14
Potassium	11·30	2·91	8·32
Sodium	1·98	0·98	3·28
Lime	4·63	5·71	18·15
Magnesium	3·84	11·47	5·45
Oxide of iron	1·44	5·22	2·10
Phosphoric acid	10·22	8·47	9·10
Sulphuric acid	1·83	1·77	2·69
Silica	62·40	62·54	50·11
Oxide of magnesium	2·13	—	—

Roger observes that the ash of the fæces of herbivora contains scarcely any alkaline carbonates.

The **amount of fæces produced** in twenty-four hours varies with the quantity and nature of the food given. We have observed that on a diet consisting of 6 kilogrammes (approximately 12 pounds) of hay, 3 kilogrammes (6 pounds) of oats, and 1½ kilogrammes (3 pounds) of bran, the average amount of fæces passed by fifteen horses during an experiment lasting seven days amounted to 14 kilogrammes (approximately 29 pounds 13 ounces) in twenty-four hours, the fæces being weighed in their natural condition—viz., containing 76 per cent. water ; the dry material of this bulk of fæces is about 3·25 kilogrammes (7¼ pounds). More fæces are passed during the night than during the day ; in the above experiment, during the twelve hours (6 p.m. to 6 a.m.), the average amount passed per horse was 9 kilogrammes (approximately 18 pounds 3 ounces), while from 6 a.m. to 6 p.m. the amount was 5·5 kilogrammes (11 pounds 10 ounces). The largest amount of fæces we have known a horse produce was an average of 33·3 kilogrammes (73·3 pounds), weighed in their natural state, in twenty-four hours ; the diet consisted of 6 kilogrammes (12 pounds) of oats, 1·5 kilogrammes (3 pounds) of bran, and 12·8 kilogrammes (28 pounds) of hay. In an experiment carried on for several months with different horses, all receiving 6 kilogrammes (12 pounds) of hay, and varying proportions of bran and oats, the average daily amount of fæces was 12 kilogrammes (24 pounds). A horse will evacuate the contents of the bowels about ten or twelve times in the twenty-four hours, and the food he consumes takes on an average four days to pass through the body.

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* Quoted by Ellenberger.

In the ox the amount of fæces is between 32 kilogrammes (70 pounds) and 37 kilogrammes (80 pounds) in the twenty-four hours. In the sheep it varies from 1 to 3 kilogrammes (2 to 6 pounds) daily; in swine 1½ to 3 kilogrammes (3 to 6 pounds), depending on the nature of the diet.

The **odour of fæces** is distinctly unpleasant, due to the presence of indol and skatol; in disease they are often extremely fœtid, and occasionally horrible.

The act of **defæcation** is performed by a contraction of the rectum, assisted by the abdominal muscles, the glottis being closed. In the horse the contraction of the rectum alone is sufficient to expel its contents; this is proved by the fact that this animal can defæcate while trotting, showing there is no necessity to fix the diaphragm and hold the breath, though at rest this does occur. In consequence the rectum of the horse can exercise extraordinary power; the hand and arm may be rendered almost numb by the pressure it can exert. The mass driven backwards under this force causes the sphincters to dilate, sometimes to an astonishing degree, and as the last trace of material is extruded, the contraction of the rectum is so great that it forces some of the mucous membrane externally, which may be temporarily imprisoned by the contracting sphincters. The muscle of the rectum receives both motor and inhibitory fibres, as previously described. Its extraordinary power in the rectum of the horse may partly be due to the horizontal position of the body; no crouching of the body occurs during the act of defæcation, such as occurs, more or less, with all other domesticated animals. The rectum has the whole work to perform single-handed, even as we have shown above, without the assistance of the diaphragm or abdominal muscles.

Two sphincters close the rectum in all animals—an external of voluntary and an internal of involuntary muscle; they are presided over by a centre in the cord. If this is destroyed, the rectum remains uncontracted, and the sphincter flabby; in the dog the cord may be destroyed in the lumbar region without interfering with the act of defæcation, which is then carried on by a reflex mechanism.

Meconium is the dark green material found in the intestines of the fœtus. It consists of biliary acids and pigments, fatty acids and cholesterin, while salts of magnesium and calcium, phosphates and sulphates, sodium chloride, soda, and potash are also found in it. Meconium is the product of liver excretion.

Pathological.

The diseases of early life in the horse are mainly situated in the chest, while those of the adult period are practically confined to the abdominal viscera, principally the intestines. The term 'colic' appears to be indissolubly associated with the horse, and it becomes a question of the greatest practical and physiological interest to ascertain the reason why digestive disturbances are so common and so frequently mortal. There are certain obvious explanations of the fact, but neither singly nor combined are the accepted ideas capable of explaining some of the mysteries surrounding the origin of these diseases.

When muscular spasms of the intestines occur, the disease is spoken of as **colic**; in many cases the pain which is exhibited is in no respect due to muscular spasm, and is only a symptom. Still, by far the majority of intestinal cases are of this kind—viz., simple muscular spasms of some part of the digestive tract, but of which part we are usually ignorant. It is obvious that either the stomach, the small or the large bowels may be so affected, but there are no definite symptoms which enable a positive diagnosis of location to be established. It is important to bear in mind the possibility of spasm of the muscular walls of the stomach, for there can be no doubt it is generally overlooked, and the intestines almost universally blamed. The evidence supporting the view we take of the liability of the stomach to disorder is afforded by the frequency of rupture of this organ, not that the rupture is due to spasm of the walls, but that the spasm is caused by stomach trouble, the rupture following as a sequel, as detailed on p. 176. It is, however, admitted that stomach spasm is far less common than spasm of the intestinal portion of the tract. We would here emphasise the facts set forth on p. 203, of the general inability of the horse to vomit, and the serious bar this proves to relief, so much so that it is hardly going too far to say that if the animal could vomit, ruptured stomach would practically be unknown, and stomach trouble generally a matter of comparatively slight importance.

In connection with intestinal trouble, we are unable to say what proportion the cases affecting the small intestines bear to those affecting the large. We cannot during life distinguish colic of the one from colic of the other. Still, there are good grounds for thinking that the large bowels are more frequently affected than the small, and for the following reasons:

1. Ingesta pass rapidly through the small intestines—so rapidly, indeed, that, as mentioned at p. 213, these bowels are nearly always found empty at ordinary post-mortem examinations, or the contents in such a fluid condition that it is not reasonable to suppose that they remain there long, from what we know of the behaviour of fluids generally in the anterior part of the digestive tract.

2. On the other hand, the large intestines always contain ingesta, for the material passes along it very slowly, so that of the three or four days occupied in accomplishing the journey from mouth to anus, all but a few hours are spent in the large intestines. It is reasonable, therefore, to assume that in cases of pure uncomplicated disordered muscular action of the bowels, the large intestine in the majority of cases is at fault.

Colic is not fatal, though Percivall described such a case. The writer's experience leads him to believe that death from a pure spasm of the bowels is unknown, and he would emphasise the point not only for the sake of accuracy, but as of value in prognosis. He believes that in any case returned as dying from colic, a more extensive search would have revealed some fatal lesion. There is no reason for believing that the pain of colic *per se* is capable of causing death.

If this be accepted—and it is fortunately capable of proof—it considerably narrows the causes of death from intestinal affections, and groups them mainly under two heads : (*a*) Inflammation of the bowels, and (*b*) displacement of the bowels.

Enteritis, by which name inflammation of the bowels is known, is spoken of as a common disease of the horse, but here again we join issue with accepted doctrines, and urge that it is an uncommon disease. Further, that in the large majority of so-called cases of enteritis, some displacement of the bowels with interference to the circulation has occurred. That uncomplicated enteritis may exist is not disputed, but we urge its relative infrequency, and press the point that what looks like inflammation is more often strangulation. When a deep purple thickened coil of intestine is found on opening the abdomen, such a case is not enteritis. The colour indicates that the blood-supply has been imprisoned as the result of strangulation, and an identical appearance would have been obtained by ligaturing the bowel. When half the double colon is found purple, thickened, filled with blood-stained fluid ingesta, the wall of the bowel being friable and its mucous membrane purple, then, however much we may be tempted to speak of it as enteritis, it certainly is not this disease, but strangulation. Enteritis must be reserved for that condition of bowel in which the mucous membrane alone is inflamed. Such a bowel may give no external indication of trouble ; the general vascular supply is not interfered with ; the full intensity of the trouble falls on the mucous membrane, and such a condition may be experimentally produced by the administration of an irritant poison. It is probable that in the horse the majority, if not all the cases, of pure enteritis met with, are due to a poison produced during the process of digestive metabolism (see p. 221). That the presence of an irritant without a poison has no such effect is abundantly proved by the pounds of sand, gravel, and calculi horses may carry in their intestines for months, perhaps years, without producing any apparent ill effect, certainly without producing enteritis. Similarly, gastritis, excepting as the result of poison, is practically unknown.

Our object in the above remarks is to focus attention on the defects in clinical observation, and to attempt a physiological analysis of the most frequent, the most fatal, and by far the most acutely painful and distressing group of diseases that any animal is exposed to. There is nothing in the whole range of comparative pathology, including the diseases of man, which compares in violence, suddenness, and mortality with digestive diseases of the horse. We have attempted to show how physiology is capable of enabling us to steer along a moderately exact course, for it is certain that unless we are agreed regarding the nature of the lesions found at post-mortem examination, we cannot reach that goal which is the object of our existence as a profession, and of which physiology is only the humble handmaid.

What is the most common cause of death among horses from intestinal affections, whether affecting the large or small bowels ? There is only one answer to this, and time and careful inquiry will prove its accuracy. The answer is **Strangulation** of the bowels, partial or complete. This strangulation is capable of physiological analysis. The most unobservant person cannot overlook a bunch of small intestines so tied together as to defy all attempts at unravelling, even when out of the body, but it takes no little careful observation to detect displacements of the large intestine.* The size, weight, and peculiar disposition of the double colon should have secured it immunity from any form of displacement ; looked at in the abdomen, it appears impossible for any force short of some mysterious power to be able to influence the position of the bowels, yet we know they are capable of being twisted as easily as if they were made of cotton. We know also that one portion may be thrust into another, in just the same way as a telescope collapses, and that a voluminous bowel like the cæcum may become completely inverted, and found within the colon, though to get there it has to pass through an opening only an inch or two wide. So remarkable, indeed, are these lesions that they cannot always be imitated after death, and, as mentioned above, it is impossible to untie many complicated knots in the small bowels, even when the organs have been removed from the abdomen.

The actual mechanism which brings about twists of the large and small intestines is disordered muscular action ; the factor responsible for telescoping intestines is disordered muscular action, and disordered muscular action is the result of disordered nervous action. For telescoping to occur, one portion of bowel must first contract until it becomes but a mere shadow of its former self ; the contracted part must then be drawn within the dilated. A different cause is at work to produce a twist of the small intestine ; this, as we previously indicated (p. 212) is tympany of the bowel, while in the case of the large intestines the muscular action must be capable of causing the bowel to perform a revolution more or less complete, and in this way reversing its position. We cannot attempt to indicate the exact disordered action which occurs ; this question would require to be worked out on the living subject. The colon and cæcum are most liberally supplied with bands (Figs. 73, 74, 76, 77, and 79), and it does not appear to us to be beyond the bounds of reasonable probability that these play a most important part in the production of displacements of the large intestines. The cause of the disordered nervous action which leads to this may, from its physiological interest, be briefly dealt with. Apart from such obvious explanations as errors in feeding (see, in this connection, pp. 180, 181, 192, 193, 257), the most common cause of derangement of the muscular action of the digestive canal is *work*. It is this which accounts for the majority of colic cases occurring towards the end of the day, the frequency with which the seizure occurs at or shortly after work, especially that of an exhausting nature, and the practical absence of colic among non-working horses. We have even known a horse in a cavalry charge rupture the ileum as completely as if the parts had been torn asunder by hand ; and this, it will be remembered, is the thickest and stoutest portion of the small intestine, and the least likely to suffer laceration. The connection between such a lesion and an exhausting gallop is at present not very apparent, but the fact is undoubted.

The whole subject is of profound practical interest, and more has been said on the matter than commonly falls to physiology to deal with, but the basis of exact clinical knowledge is sound anatomy and physiology, and we feel that the physiological aspect of digestive disorders has not yet received adequate attention. We must bear in mind that the whole length of the digestive tract is a chemical laboratory concerned in the analysis of food-stuffs, isolating and retaining those which are of use, getting rid of those which are useless, and rendering harmless those substances capable of acting injuriously. Not only is it a laboratory where the above analytical operations are carried out, but it is also a factory where the chemical reagents necessary for this process are prepared beforehand. So thoroughly is the analysis performed, that the most complex bodies are broken down into the simplest products. Can it be wondered at that the chemical processes may sometimes fail, and disorder result ?

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* From the point of view of equine pathology, one of the most valuable contributions made to veterinary literature by the late Professor Walley was his account of displacements of the colon in the horse (*Veterinary Journal*, vol. ix.). It was the first time in this country that the possibility of these immense bowels being twisted and displaced was ever described.

We see a faithful reflex of the laboratory processes in the disorders of the canal, the **diarrhœa** which is full of beneficence, **impaction** which indicates a loss of muscular power and physical alteration of the contents, acute **tympany** which announces active fermentation, **rupture** which indicates the strain on the walls of the apparatus; these, and others too numerous to be dealt with, and which no mere mention explains, give some idea of the penalty paid by horses for the doubtful privilege of domestication. The term ' digestion of a horse ' has been framed in absolute ignorance of the real facts. There is no animal in which these organs are more readily disturbed, and none in which they are the subject of such acutely painful and mortal lesions.

The ruminant, from the peculiarity of its physiological arrangement, is far more liable to stomach than intestinal trouble ; **tympany**. **impaction, paralysis,** and **inflammation** of one or more of the compartments are common. In spite of the size of the œsophagus, impaction is frequent, in marked contrast to the horse, in which it is uncommon, while **calculi,** a special feature in the intestine of the horse, are found in the stomach of the ox, though brought about by very different causes. **Strangulation** of the bowels in the ox is not unknown, but limited to a special variety due to anatomical conditions. **Parasitic** trouble in all animals is a prominent pathological feature, the digestive canal from the mouth to the anus being liable to infection with numerous varieties of parasites, and it also forms the main channel of parasitic entry for other parts of the body.

CHAPTER VI

THE LIVER AND PANCREAS

SECTION I.

The Liver.

IN considering the function of the liver it is necessary to bear in mind its peculiar blood supply. Most glands of the body which are called upon to produce a secretion are furnished only with arterial blood for the purpose, but the liver is an exception to this rule ; the entire venous blood returning from the splanchnic area—viz., the bowels, stomach, spleen, pancreas, etc.—constitutes the material with which the liver is flooded. Such a mixture of blood derived from a peculiar and considerable area must be charged with many products, some the result of secretory activity, others the soluble constituents of the elements of food ; or, again, substances absorbed from the intestinal canal, which are by-products produced during the gradual breaking-down of the food substances. It is from this blood that the liver performs its various functions, and one of the most evident—viz., the secretion of bile—will be dealt with first.

Bile.

The bile is a fluid of an alkaline reaction, bitter taste, a specific gravity in the ox of 1022 to 1025, in the sheep from 1025 to 1031, and in the horse 1005. The colour is yellowish-green or dark green in herbivora, reddish-brown in the pig, and golden-red in carnivora. These differences in colour depend upon the character of the pigment present. Bile taken direct from the liver is relatively watery in consistence ; that taken from the gall-bladder is viscid, due to admixture with nucleo-albumin during its stay in the latter receptacle. The secretion contains no protein, which is somewhat remarkable ; biliary pigments, bile acids, fats, soaps, lecithin, cholesterin, and inorganic salts are found in varying quantities. By standing in the gall-bladder the solids are considerably increased, owing to an absorption of part of the water of the bile. The secretion in the horse contains no mucin, and, according to Ellenberger, there is very little mucin in the bile of sheep; what was believed to be mucin in ox bile, which conferred on the latter its ropy character, is now known to be nucleo-albumin.

The dried alcoholic extract of bile contains in the ox 3·58 per cent. of sulphur, sheep, 5·71 per cent., and pig, 0·33 per cent. The gases found in bile are CO_2, and traces of O and N. The chief inorganic salts are sodium chloride and phosphate, besides which are found salts of calcium, magnesium, potassium, iron, with phosphoric and sulphuric acids; the sodium salts always exist in the largest proportion. The iron, which is found as phosphate, is probably derived from the hæmoglobin of the blood during the formation of the bile pigments.

The following table, showing the percentage composition of various biles, is mainly compiled from Ellenberger:

	Horse Bile.	Ox Bile.	Dog Bile.	Pig Bile.
Water - -	95	92·91	95·3	88·8
Solids - -	5	9·60	4·7	1·2
Bile acids Bile pigments Fat Mucin -	—	8·30	4·1	10·1
Salts - - -	—	1·30	0·6	1·1

Percentage Composition of the Ash of Ox Bile.

Sodium chloride - -	27·70	Manganese peroxide -	0·12
Potassium - - -	4·80	Phosphoric acid - -	10·45
Sodium - - -	36·70	Sulphuric acid - -	6·39
Calcium carbonate -	1·40	Carbonic acid - -	11·26
Magnesium - - -	0·53	Silica - - - -	0·36
Iron oxide - - -	0·23		

The differences found in the composition of bile probably depend upon whether it be taken from the gall-bladder or from a fistula, the former being the more concentrated.

The **Bile Pigments** are two in number—**bilirubin** and **biliverdin**; the latter is produced by oxidation from the former. Bilirubin is the colouring matter of human bile and that of carnivora, whilst biliverdin is the pigment of the bile of herbivora. It is not uncommon to find both pigments in the same specimen of bile. Though the bile of the dog contains exclusively bilirubin as a pigment, yet the placenta of this animal is rich in biliverdin. In the ox and sheep a pigment is present in bile which shows first a three-banded, and later, on standing, a four-banded spectrum. These bands are due to **cholohæmatin,** which is not a bile pigment proper. The pigments are insoluble in water, but soluble in alkalies ; in the bile they are held in solution by the bile acids and alkalies. Bilirubin may be obtained from the gall-stones of the ox in the form of an orange-coloured powder, which can be made to crystallise in rhombic tablets and prisms. If an alkaline solution of bilirubin be exposed to the air, it becomes biliverdin by oxidation, and this latter pigment, by appropriate treatment, may be obtained as a green powder. Both colouring matters of the bile behave like acids, forming soluble compounds with metals of the potassium group, insoluble ones with those of the calcium group (Bunge).

On the addition of nitric acid (containing nitrous acid) to the bile pigments a play of colour is observed ; this is known as Gmelin's test. In the case of bilirubin the colours pass from yellowish-red to green, then to blue, violet, red, and yellow ; each of these colours is indicative of a different degree of oxidation of the original bilirubin. Biliverdin gives the same play of colours, excepting the initial yellowish-red, which is absent.

Although bilirubin has not been obtained from hæmoglobin, there is no doubt that this is the source of the pigment, for if hæmoglobin be liberated in the blood and enters the plasma, bile pigments appear in the urine ; further, hæmoglobin may be readily decomposed, yielding a protein and hæmatin ; and if this hæmatin be deprived of iron, the residue thus obtained is not very dissimilar in composition to bilirubin. We have previously mentioned (p. 13) that old blood-clots contain an iron-free substance known as hæmatoidin, and this is practically identical in composition with bilirubin. When red blood-cells disintegrate in the ordinary course of their wear and tear, the liberated hæmoglobin is brought to the liver, and under the influence of the liver cells converted into the iron-free substance bilirubin or biliverdin. Part of the iron so liberated escapes from the body through the bile, but the bulk of it is retained, and again used in the formation of hæmoglobin by the organs which discharge this function.

Though biliverdin is the colouring matter of the bile of herbivora, yet the gall-stones found in the ox consist very largely of bilirubin combined with chalk ; in the pig the same combination is observed. Bilirubin is said by Hammarsten to be constantly present in the serum from horse's blood, though not in that of the ox, and Salkowski states that it is a normal constituent of the urine of the dog during the summer. In the large intestines both bilirubin and biliverdin undergo reduction, resulting in the formation of **stercobilin,** the colouring matter of the fæces in some animals. It is possible also that some of the pigment is reabsorbed from the intestinal canal, carried to the liver, and again eliminated. The value of this circulation of bile pigment is unknown.

The **Bile Salts** are two in number—**glycocholate** and **taurocholate of soda**; they are formed in the liver by the union of **cholalic acid** with **glycin** or **taurin,** and exist in combination with soda. These salts are found in varying proportions in different animals; thus, glycocholate of soda is largely found in herbivora, taurocholate principally in carnivora, while in the pig hyoglycocholic and hyotaurocholic acids are found. Both salts are soluble in water, have a markedly alkaline reaction, rotate the plane of polarised light to the right, and may be obtained in a crystalline form as highly deliquescent acicular needles. Glycocholic acid is the chief bile acid in herbivora; it is produced by the union of glycin with cholalic acid; it is diminished by an animal and increased by a vegetable diet. Taurocholic acid is produced from taurin and cholalic acid, and exists principally in carnivora, though small quantities may be found in the ox. This acid differs from the first characteristically by containing sulphur, by which it shows its proteid origin. Glycin or glycocoll also owes its origin to the proteids of the food, and if administered it reappears externally as urea. It cannot be traced in the free state in the body, but occurs in the urine combined with benzoic acid, in the form of hippuric acid. Pettenkofer's test for bile acids is performed as follows: A drop of the fluid is placed on a white earthenware surface, and to it is added a drop of a strong (10 to 20 per cent.) solution of cane sugar, and a similar quantity of strong sulphuric acid; a beautiful purple-red colour forms. The colour is due to **furfurol,** and is produced by the action of the acids on the sugar and the subsequent reaction with cholalic acid.

The **origin of the bile acids** is involved in obscurity; taurin may be formed from **cystin,** and this is capable of yielding taurin on oxidation; cystin is an end-product of protein disintegration; glycin may also be formed from protein. The precursors of cholalic acid are unknown; nor do we know why glycin should predominate in some animals and taurin in others. It appears clear that the bile salts are formed in the liver cells. In the intestines a portion of the bile salts is reabsorbed, carried to the liver, and again excreted; or they may be split up in the intestines into their constituents, the glycin and taurin being carried to the liver to be reutilised, while the cholalic acid is excreted. This economical measure, the second of its kind noted in connection with the liver, has a twofold advantage, for not only can the glycin and taurin be used over and over again, but the bile acids are the best of cholagogues, and stimulate the production of bile.

Cholesterin finds its way to the liver for the purpose of being excreted. It is a substance found in many of the tissues of the body, but especially in the white matter of the nervous system. It is insoluble in water, but soluble in a solution of bile acids. When cholesterin finds its way into the bile, it is eliminated with the fæces. Cholesterin is found in very regular quantities in the body, and forms one of the principal constituents of certain gall-stones, and also, it may be added, of tumours in the lateral ventricle of the brain of the horse.

Lecithin is another waste product brought to the liver for excretion. It is of unknown physiological significance, but it has been suggested that it may serve to activate the lipase of the pancreatic secretion.

Secretion of Bile.—Bile is secreted under a very low pressure, which is the reverse of what occurs in the saliva ; low as the pressure is—13 mm. (0·58 inch) of mercury—it is higher than that of the blood in the portal vein. If the pressure in the bile-duct be raised, the bile is reabsorbed, being taken up by the lymphatics of the liver, and so conveyed to the blood-stream. It is probable that the majority of cases of jaundice are due to obstructive causes, though exceptions to this rule occur. The secretion of bile is a continuous one ; whether the animal be in full digestion or fasting, the flow is not intermittent, as in the case of the saliva. Though continuous, it is not uniform ; it reaches its maximum in the dog between the second and fourth hours after a meal ; this is followed by a fall, and again about the seventh hour by a rise. A similar curve is given by the pancreatic secretion, which suggests how closely these two fluids are co-operative in digestion, while it can be shown that a specific substance, *secretin*, which stimulates the production of pancreatic juice, also hastens the secretion of bile. Acids injected into the duodenum increase the flow of bile, even after all nervous connections are severed. This is due to the acid chyme converting the *pro-secretin* into secretin, and this, as above stated, has a specific action on the liver cells.

The secretion of bile is increased by any agent which destroys the red blood-cells. A solution of hæmoglobin injected into the blood produces the same effect. The administration of bile increases its production ; this is due to the bile acids having a specific action on the liver cells, and acting as cholagogues.

In those animals possessing a gall-bladder this receptacle is filled with bile during abstinence, or, if it be empty, it is filled even during digestion. The reflux of bile from the biliary duct to the gall-bladder is caused by a sphincter-like contraction of that portion of the duct penetrating the wall of the intestine, by which means the bile is driven back through the cystic duct to the gall-bladder. The bile as formed is propelled along the bile-ducts by a contraction of the muscular coat of the tubes, but doubtless both the forcing onward of the bile and the circulation through the liver are largely assisted by the respiratory movements, during which the liver is compressed between the abdominal viscera and the diaphragm.

By some it is considered that no bile enters the bowel while the stomach is empty, but that the passage of acid chyme along the duodenum causes a reflex contraction of the gall-bladder, and an injection of bile into the intestine.

The **amount of bile** secreted varies, but is greater in herbivora than carnivora. Colin's experiments gave him the following amounts as hourly secretions :

Horse	-	250 to 310	grammes	(8 to 10 ounces) per hour.
Ox	-	93 to 120	,,	(3 to 4 ounces) per hour.
Sheep	-	8 to 150	,,	(¼ ounce to 5 ounces) per hour.
Pig	-	62 to 150	,,	(2 to 5 ounces) per hour.
Dog	-	8 to 16	,,	(¼ to ½ ounce) per hour.

The **Use of the Bile** from a digestive point of view is disappointing, inasmuch as it does not digest in the same sense that pepsin and trypsin do. It is intimately connected with the function of the pancreas, with which object the secretions are poured out either close together in the bowel, or, as in some animals, by a duct practically common to the two glands. As the horse possesses no gall-bladder, the secretion is poured into the intestine as fast as it is prepared ; not so with the ox, sheep, pig, and dog, where the bulk of it is stored up in a capacious receptacle until required. The reason offered for the horse having no gall-bladder is that as digestion, under ordinary circumstances, never ceases, the bile is poured into the bowel as fast as it is secreted, but that in the case of other animals it is only poured out when the contents of the stomach are passing out into the intestine. This explanation, however, does not meet all the difficulties of the case. The following animals, like the horse, have no gall-bladder : the camel, elephant, rhinoceros, tapir, and deer.

The bile being alkaline, its first action on the chyme is to neutralise the gastric juice, and precipitate the albumoses and peptones. One effect of this is probably to delay the progress of the chyme along the bowel, by which means absorption is assisted.

Bile has a solvent and emulsifying effect on fats, being more active in the presence than in the absence of pancreatic juice.

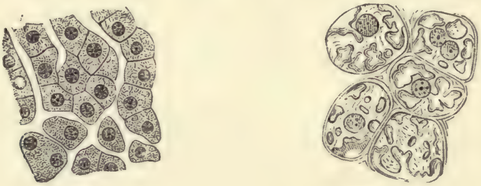
Bile cannot split up fats into fatty acids and glycerin, as the pancreas does, but its presence increases threefold the action of the pancreatic fluid in this respect. Once the fats are split, the bile takes an active share, for fatty acids, which are insoluble in water, are soluble in bile salts and lecithin, the latter greatly increasing the power of the bile salts as fat solvents. The fatty acid forms soaps with the alkali of the intestinal and pancreatic secretion, and these are also dissolved by the bile acids. The solution of soaps so formed makes the emulsifying effect of the bile permanent and absorption of fat easier. In Voit's experiments on dogs it was found that by cutting off the flow of bile to the intestine the absorption of fat fell from 99 per cent. to 40 per cent. ; the solvent action of bile on fat is the chief digestive function of this fluid, but in its action on fat it works in conjunction with the pancreatic secretion. We shall see later (p. 256) how the presence of bile increases the energy of the pancreatic fluid in the emulsification of fat. Bile has no action on proteins. According to Hofmeister, the bile of the ox, sheep, and horse converts starch into sugar, while the bile of the pig and dog possesses no such power, or only to a limited extent. It has been said that bile has an antiseptic influence on the intestinal contents, protecting them from putrefaction and promoting peristalsis ; for it has been found that when it is prevented from entering the bowels, constipation and extreme fœtor of the intestinal contents result. Bile, however, is not a true antiseptic. The clay-coloured fæces obtained in jaundice are probably due to the presence of unacted-on fat ; the fat encloses the proteids which putrefy, hence the odour. The bile acts as a natural purgative, and keeps up intestinal peristalsis ; by so doing it hurries the food residues out of the system before they undergo putrefactive decomposition.

Glycogen.

It is quite certain that the largest gland in the body must have some other function than that of the secretion of a fluid of comparatively unimportant digestive power, and such is the case ; the liver manufactures and stores up in its cells a peculiar substance known as glycogen or animal starch. Glycogen is spoken of as a starch, though it differs from vegetable starch in many important characteristics ; thus, it is soluble instead of insoluble in cold water, and it is stained reddish-brown instead of blue by iodine. Though glycogen may be detected in the liver substance by the iodine test, it is now believed that it is not actually deposited in the cells, but held there in weak chemical combination ; for it cannot readily be extracted from the liver by means of cold water, whereas outside the body it is readily soluble in water.

The literature of the formation and use of glycogen is extensive, perhaps no substance has given rise to greater controversy ; yet the glycogen story which is accepted to-day is the one originally related by Claude Bernard, who was the discoverer of this singular substance.

The sugar in the food, and that derived from starch-conversion, finds its way by means of the intestinal vessels into the portal vein, which, depending on the nature of the diet, contains varying proportions of sugar, and from here it passes into the liver ; under ordinary circumstances, it is stored up in the liver as glycogen, being, in fact, reconverted into a kind of starch, and gradually doled out by the hepatic veins to the system as sugar when required. The liver regulates the amount of sugar which should pass into the blood ; so much, and no more, is admitted to the circulating fluid, the amount varying between 0·05 and 0·15 per cent. The sugar in the blood of the ox was estimated by C. Bernard at 0·17 per cent., in the calf 0·1 per cent., and in the horse 0·09 per cent. There is consequently a great difference between the sugar content of the portal and that of the hepatic vein. When the liver fails to regulate the amount of sugar in the blood diabetes is produced, and this occurs when the amount of sugar rises to more than 0·2 per cent.



FASTING. AFTER FOOD.

FIG. 82.—LIVER CELLS FROM THE DOG DURING FASTING AND AFTER FOOD (WALLER, AFTER HEIDENHAIN).

During fasting the cells contain no glycogen ; after receiving food they become swollen with this substance.

The glycogen which is stored up in the liver for future use may in two or more days be made to disappear by starving and *working* the animal, the material in this way escaping from the liver as sugar, and passing into the general circulation through the hepatic veins. The administration of arsenic or phosphorus, by their action on the liver cells, also causes a marked diminution in the amount of glycogen, while strychnine in poisonous doses is most effective in this respect, owing to the excessive muscular contractions produced.

The storing up of glycogen by the liver and its subsequent utilisation is very closely allied to a similar process in the vegetable kingdom; the starch in the leaves of plants may pass down the stem as sugar for the purpose of nourishment, and be again formed into starch. Similarly in the animal the starch must be first converted into sugar before the bloodvessels of the bowel can take it up, then in the liver once more converted into glycogen, and lastly, again, into sugar before being finally used by the tissues. The sugar formed from starch in the bowel is maltose, while that formed in the liver from glycogen is dextrose. This conversion of glycogen into dextrose is due to the presence of a ferment in the liver cells.

The total amount of glycogen obtained from a given quantity of food is not wholly stored in the liver; the latter organ can only hold a limited amount, which in the dog, by a rich carbohydrate diet, does not exceed 17 per cent., and in the rabbit 27 per cent., of its weight, and in other animals is less. We know, as a fact, that the liver, having taken up all the sugar it can from the portal vessels and converted it into stored-up glycogen, allows the balance to pass through the hepatic veins into the general circulation as sugar, and that it is deposited in other organs, principally the muscles, as glycogen for future use. The muscles of well-fed animals contain in this way a considerable quantity of glycogen; even after nine days' starvation in the horse from 1 to 2·4 per cent. has been found. Ordinarily it may be stated that the muscles hold as much glycogen as the liver, but it takes longer by means of work and starvation to free the muscles from glycogen than to clear the liver. The presence of glycogen in muscle is not essential to contraction, for there are muscles in which no glycogen is found, and yet in which active contraction takes place. In the muscles of the embryo, before striation has occurred, the amount of glycogen existing is something considerable; as much as 40 per cent. of the dry material of the embryo muscle may consist of this substance. As striation appears the glycogen leaves the muscles to a great extent, and the liver takes on the process of production.

The Use of Glycogen.—The muscles and liver are not the exclusive seats of glycogen deposits; traces may be found practically everywhere in the body, but none can be found in the blood plasma. The existence of glycogen in the embryonic muscle points to its use in active nutrition and rapid growth; further, it is found in the placenta, where it is used for the nourishment of the fœtus. In the adult the chief use of glycogen is to facilitate the metabolic production of muscular energy and animal heat, and this is effected by the oxidation of dextrose to carbon dioxide and water. This oxidation does not occur in the blood; the destruction of sugar (*glycolysis*) occurs in all active tissues, especially muscles and glands. It can be shown that there is less sugar in the veins of an active muscle than in the arterial blood supplying it. The muscles of the upper lip of the horse used up in a state of activity 3·5 times more dextrose than during rest, and the actively secreting parotid gland of the same animal used more sugar than the resting gland.

The **sources of glycogen** have been a fertile cause of discussion and object of experimental inquiry. It was natural to consider, as we have so far done, carbohydrate material as the chief contributing agent; it was less certain whether proteins contributed, while the consensus of opinion was against fat taking any share in the process. We must examine each of these in a little more detail.

We have learnt that starch is not absorbed as starch, but, depending upon the nature of the diastatic ferment, is converted into maltose, or maltose and some dextrin, and subsequently dextrose. These sugars are readily converted into glycogen by the liver cells by the process of dehydration. Cane sugar and milk sugar are not readily converted into glycogen, but since these double sugars undergo inversion in the intestinal canal before absorption—cane sugar into dextrose and levulose, and milk sugar into dextrose and galactose—they may in this form be readily converted into glycogen. All carbohydrates, then (with the exception of lactose), which are capable of being changed into dextrose or levulose, may be converted into glycogen, provided they pass through the laboratory of the intestinal canal. For example, cane sugar, if injected subcutaneously, passes unchanged into the urine; in order to be converted into glycogen it must pass through the intestine.

The effect of protein on glycogen formation is not so easily settled. It is observed that in diabetes, though all carbohydrate food be withheld, yet sugar may appear in the urine on an exclusively protein diet; the same thing is observed in the experimental glycosuria which may be produced by the administration of a substance known as 'phloridzin,'* and, furthermore, that sugar may be produced even when the animal is starved. The conclusion appears irresistible that protein can produce sugar, and this is explained by saying that certain proteins split into a nitrogenous and non-nitrogenous portion, the former being converted into urea, while the non-nitrogenous residue is converted into sugar, and may thus give rise to glycogen. It is now known, however, that proteins which do not contain a carbohydrate group, such as casein, may take a share in the production of glycogen; this strengthens the belief that protein may give rise to sugar. But apart from the carbohydrate portion of the protein molecule as a source of glycogen, it is now known that sugar can

* Obtained from the roots of the apple-tree.

be formed from some of the end-products of the pancreatic digestion of proteins (p. 255)—viz., the amino-bodies—of which *glycin* and *alanin* may be completely converted into dextrose, and *glutamic* and *aspartic* acids partly so converted.

There are a few observers who regard fat as a source of glycogen, and there is some evidence to show that it may contribute, for it has been said that glycerin acts as a sugar former. If this is so the conversion of fat into glycogen, through its splitting up in the intestinal canal into fatty acid and glycerin, would not be a difficult matter. On the other hand, experiment shows that when an animal is fed solely on fat, the glycogen disappears from the liver as quickly as it does in starvation. Nevertheless, it is an interesting fact that during prolonged starvation, even forty to ninety days, the amount of sugar in the blood is practically constant, and its only sources at this time are the proteins and fat of the body. The question is, therefore, very far from being settled.

The Liver Ferment.—When a liver is rapidly removed from the body of a recently killed animal which has been appropriately fed, it contains a quantity of glycogen ; if it is allowed to stand the glycogen gradually becomes reduced in amount, and sugar takes its place ; finally all the glycogen disappears. This change is brought about by a diastatic ferment in the liver cells which changes the glycogen into sugar. If the liver on removal from the body be rapidly minced and boiled, the ferment is destroyed, and dextrose is not formed.

How the Supply of Sugar is Regulated.—We have seen that in the tissues the glycogen in the form of dextrose is oxidised into carbon dioxide and water, resulting in heat and energy. After every meal a store of glycogen accumulates in the liver for subsequent use, and in spite of changes in the amount of diet, difference in the amount of daily work performed, or of heat produced, yet the sugar in the hepatic veins maintains a perfectly regular proportion of from 0·1 to 0·2 per cent. The means which control the issue of sugar from the liver are very imperfectly known ; they are probably under the influence of both the nervous system and of an *internal secretion* produced by the pancreas, and the subject will be again considered when the pancreas is dealt with. One thing seems clear—that the liver itself is unable to regulate the amount, and that whenever either the nervous or chemical factors fail, it allows sugar to pass into the blood in a proportion largely over and above that which can be oxidised (*hyperglycemia*), with the result that it escapes with the urine (*glycosuria*), constituting the disease known as **diabetes.** The sugar excreted with the urine is, of course, lost to the system, and constitutes a heavy drain on the body, which in consequence rapidly wastes. This condition may be experimentally produced in the dog by the removal of the pancreas, which renders the animal diabetic; and though we are anticipating matters, as this question must again be considered in dealing with that organ, it may here be stated that the removal of the pancreas produces diabetes, for the reason that the internal secretion of that gland, which is referred to above, activates a pro-ferment in the muscles, by which means the sugar is oxidised.

Further Uses of the Liver.

We have studied two uses of the liver—viz., the formation of bile and the storing up of glycogen—but there are other functions of this gland to consider.

The Formation of Urea.—When the complex protein molecule of the food is broken down into simpler end-products, one of these, known as 'urea,' is excreted by means of the kidneys; this substance, however, is not formed in these organs. It is proved conclusively that part, at least, of the urea in the body is formed in the liver. During the process of protein disintegration certain amino acids, known as *leucine* and *tyrosine*, are produced, either in the intestinal canal under the influence of pancreatic digestion, or in the living cell as the result of the breaking down of protein. Under any circumstances the leucine undergoes a series of oxidative changes mainly in the liver, which result in the formation of urea.

The further facts regarding the formation of urea are best dealt with in the section devoted to the kidneys.

As the result of protein decomposition in the intestinal canal certain aromatic compounds are formed; these are united with sulphuric acid, and got rid of by the kidneys as conjugated sulphuric acids. In this combination the originally *poisonous protein products* are converted into non-poisonous ones, and this change is effected in the liver (Bunge). In this we have a very important function of the liver demonstrated—viz., as a neutraliser of poisons introduced into the blood by the intestines. It is a noteworthy fact that many metallic poisons are also arrested in the liver—for example, mercury and arsenic.

The numerous and complicated changes produced by the liver may thus be summarised: It forms bile, regulates the supply of sugar to the system, and stores up as glycogen what is not required. It guards the systemic circulation against the introduction of certain nitrogenous poisons, such as ammonia, by transforming them into urea, and against other poisons of protein origin by converting them into harmless products, by conjugation with alkaline sulphates.

SECTION 2.

The Pancreas.

The fluid secreted by the pancreas performs certain important functions in digestion. It has been remarked that there is scarcely any animal which does not possess a secretion allied to the pancreatic; even those invertebrates without a peptic or biliary apparatus are in possession of one. From the resemblance of the pancreas to the salivary glands, it has been termed the 'abdominal salivary gland.'

The pancreatic fluid from herbivora can only be obtained with extreme difficulty; to establish a pancreatic fistula in the horse is a formidable operation, necessitating an incision from the sternum to the pubis and the turning back of the bowels. Colin has established these fistulæ both in the horse and ox, but the profound impression on the nervous system produced by such extensive interference must considerably affect the character of the secretion and the amount manufactured.

Pancreatic fluid is an alkaline, clear, colourless fluid like water, and though viscid in some animals is not so in the horse or ox. It has a saltish, unpleasant taste, and a specific gravity of about 1010; the viscid secretion of the dog has a specific gravity of 1030. The following analysis of the fluid in the horse is given by Hoppe-Seyler:

Water -	98·25			
Solids -	1·74	Organic matter -	0·88,	containing 0·86 of ferments.
		Salts - -	0·86,	containing much sodium phosphate.
	100·00			

Schmidt found the fluid of the dog to have the following composition:

Water -	90·00			
Solids -	9·92	Organic matter -	9·04	
		Salts - -	0·88,	containing much sodium chloride.

The salts present are sodium chloride in abundance, potassium chloride in traces, sodium carbonate and phosphate, calcium and magnesium phosphates in small quantities. To the sodium carbonate is due the strong alkaline reaction. The organic solids are remarkable for the amount of protein present in them; they vary in amount in different animals—for example, 9 per cent. in the dog, and 0·9 per cent. in the horse. In addition to these, the pancreatic secretion is remarkable for containing three enzymes, which act on different food substances.

Mechanism of Pancreatic Secretion.—The pancreatic secretion is influenced by special secretory nerves; stimulation of the vagus or splanchnic may, after a long latent period, give rise to a secretion, though it is not yet settled whether these fibres produce it during the act of digestion. The outpouring of the acid chyme from the stomach into the duodenum at once gives rise to a secretion of pancreatic juice, and at one time it was supposed the acid acted on the secretory nerves and produced a secretion reflexly, for this action could be reproduced experimentally. Bayliss and Starling, however, demonstrated the remarkable fact that if an extract of the mucous membrane of the duodenum or jejunum be made by scraping the bowel, and acting on it by weak hydrochloric acid, a substance may be obtained which when injected into the blood produces a profuse pancreatic secretion. To this internal secretion of the intestinal cells they gave the name **Secretin,** the nature of which has not been determined. Two facts are clearly established—first, that it is not a ferment, as it is not destroyed by boiling; and, secondly, that acid is an essential part of the process, for if the mucous membrane of the bowel be extracted with either water or saline solution, secretin is not obtained. It is the *acid* chyme, therefore, acting on the mucous membrane of the intestine which produces secretin; this is absorbed by the blood, and thus produces its specific action on the pancreas. Within a minute or two of introducing a 0·4 per cent. hydrochloric acid into the duodenum pancreatic juice flows into the intestine. The acid produces the same effect if introduced into the jejunum, but not into the ileum.

Secretin is not a protein; it is not destroyed, as stated above, by boiling, and it is soluble in alcohol and ether. Prosecretin exists in the intestinal mucous membrane; it may be extracted with physiological salt solution, and though unable itself to promote pancreatic secretion, it may be converted into an active secretion by the action of acid or by boiling. Secretin from one animal will increase the pancreatic flow in another, either of the same or of a different species.

As a secretion can be obtained from the pancreas either by stimulation of certain nerves or by introducing into the blood a specific chemical substance, it would appear that under normal conditions both processes may be operating in its production, and that there may be, as in the case of the gastric juice, two parts in the secretion. Evidence has been brought forward to show that the secretions obtained from these two sources differ considerably. The nervous secretion is thick, rich in ferments, poor in alkali. The trypsin it contains is active, and the effect of atropine is to suspend secretion, while that of pilocarpine is to stimulate it. The chemically produced fluid is thin and watery, contains but a small amount of ferment, and an abundance of alkali. The secretion is unaffected by atropine, and its trypsin is not in an active form when secreted.

Uses of the Secretion.—The pancreatic juice is poured into the bowel in the horse and sheep by an opening common to the pancreas and liver, while in the ox, pig, and dog, the ducts of the liver and pancreas are separate, and open within a short distance of each other.

It is essentially a digestive fluid, and acts on the three classes of food-stuffs—viz., proteins, fats, and carbohydrates. To enable this to be effected, it contains three ferments or their precursors—viz.:

A Proteolytic Enzyme which acts on proteins (*Trypsin*).
A Diastatic Enzyme which acts on carbohydrates (*Amylopsin*).
A Lipolytic Enzyme which acts on fats (*Lipase or Steapsin*).

Observations appear to show that the proportion of each of these ferments in the secretion depends on the character of the food; if, for example, the food is rich in fat, the secretion would be rich in lipase. It is also probable that not only does the nature of the food determine the predominance of each enzyme, but also the amount of fluid to be secreted. This, as a rule, reaches its maximum in the dog between the second and fourth hour after taking food, and corresponds to the greatest activity of the liver. In dogs which have been starved active secretion of bile, pancreatic juice, and intestinal fluid, associated with gastro-intestinal movements (see p. 226), take place, it is said, every two hours, and last for twenty minutes. The cause of this is by no means clear. All the fluid thus poured out is reabsorbed.

Trypsin.—It has been observed that pancreatic juice taken direct from a fistula in the duct may have little or no action on the proteins of food, but if the same fluid be allowed to become contaminated by the intestinal contents it at once becomes active. Evidently the addition of a something from the bowel has brought about a marked change in the proteolytic character of the secretion. Investigation shows that though the secretion taken direct from the pancreas contains the precursor of trypsin—viz., **trypsinogen**—yet in the latter form the ferment is unable to act on the protein of food until it has itself been acted upon by another ferment. This ferment is derived from the mucous membrane of the intestinal canal. A ferment acting on a ferment has been described as a **kinase,** and as this one is derived from the bowel it is called **enterokinase,** a very small amount of which is capable of converting inactive trypsinogen into active trypsin. It is remarkable that of the three ferments secreted by the pancreas, trypsin is the only one which is secreted in an inactive condition. Pawlow considers this to be due to the fact that if trypsin were active *in* the pancreatic juice, it would destroy its fellow-ferments, but that in the bowel these ferments are protected.

The fact that extracts of pancreas, as obtained usually from a slaughter-house, may be made more tryptically active by the addition of a little dilute acetic acid, does not now imply that the acid has converted the trypsinogen into trypsin, as has usually been supposed. The pancreas used in the preparation of the extracts is already contaminated with minute quantities of enterokinase, whose activity is greatly increased by neutralising the alkalinity of the extracts. If a pancreas be obtained under conditions which insure the absence of any admixture with even traces of enterokinase, extracts of such a pancreas cannot be rendered more tryptically active by the addition of dilute acid (Starling). It is now believed that the conversion of inactive to active trypsin may be effected by salts of calcium and magnesium, as well as by enterokinase.

The action of trypsin on proteins is most interesting. The protein molecule is very complex ; the use of trypsin is to split it up into simpler products, with the object of facilitating its absorption. As we shall point out later, no food substance is taken up excepting in its simpler form, and the proteins of oats, barley, hay, or flesh, have to be reconstructed in order to form part of the tissues of the living animal. To enable this to be done trypsin acts on the large protein molecule, and breaks it down in the production of a number of simpler bodies of smaller molecular weight ; on these the tissue-cells set to work, and by a process of synthesis construct the form of protein needed by the body. It can be easily shown that the action of trypsin on protein is much more satisfactory and thorough if the latter has previously been acted upon by pepsin. Trypsin, like pepsin, produces albumose and peptones ; but the process does not stop at peptone ; no peptone can be found in the blood, and none remains after a prolonged pancreatic digestion. The action of trypsin on proteins is nearly as complete as boiling protein with acid. In each case the hydrolysis results in the production of a large number of simpler end-products, chiefly of amino-bodies. Yet it would appear clear that the products obtained by acid hydrolysis are not quite the same as those produced by tryptic hydrolysis, for dogs may be kept in health when fed on the split products of pancreatic digestion, with a sufficiency of carbohydrates and fat, while the split products of acid hydrolysis cannot be so utilised. The question will be considered again in dealing with nutrition, but the matter is of interest here as showing that the laboratory of the body reduces the complex protein molecule into many simpler substances, which can be reproduced outside the body by active chemical means, and yet are not quite the same, for the material artificially produced by means of boiling acid is of no subsequent use to the body, whereas that produced in the system can be utilised.

The amino-bodies resulting from tryptic digestion are mainly organic acids containing either one amino (NH_2) group, or two such groups in union with carbon. Among the mon-amino-bodies are leucine, tyrosine, glycine, aspartic acid, glutaminic acid, and tryptophan. Of the diamino-bodies, lysin, arginin, and histidin are present.

It should be stated that another view regarding the breaking down of protein into simpler substances exists—viz., that the whole protein molecule is not split up by tryptic digestion, but that a nucleus remains which in chemical character comes between a peptone and amino-bodies. It is described as a *peptid*, or more generally as *polypeptid*, as it is probable that it is not a simple body. The polypeptid may by acid hydrolysis be converted into amino-bodies. It is suggested that the production of polypeptids serves as a starting-point for synthesis, for the protein substances taken in as food have to become converted into the tissues of the living animal, reconstructed in part from the amino-bodies, and the necessary synthesis, it is suggested, occurs around, or is directed by, the polypeptids. Whether this is necessary or no does not in any way affect the important statement that all protein received as food is foreign to the body, and that before it can be built into the tissues of the living animal it has first to be pulled to pieces, and then again built up.

Should any protein or peptone have escaped the action of pepsin and trypsin, it may be attacked by another enzyme found in the intestinal mucous membrane, known as **erepsin,** which also has the power of breaking down albumoses and peptones into leucine and tyrosine. Erepsin is found in most of the tissues of the body, so is not specific to the intestine.

Under the influence of bacterial action numerous decomposition products may be split off from protein; among others aromatic bodies are formed—phenol, indol, and skatol, the latter being responsible for the fæcal odour of a pancreatic digestion mixture. These substances are produced from tryptophan, one of the end-products of the primary decomposition of proteins.

It is here desirable to draw attention to the fact that *secretin, enterokinase,* and *erepsin* are all derived from the mucous membrane of the intestinal canal, and care must be taken to avoid confusing them: the second and last are ferments, secretin is not. The function of secretin is to cause the production of pancreatic juice, that of enterokinase is to endow one of the ferments of the pancreatic juice with its remarkable proteolytic properties, while erepsin breaks down albumose, and peptones into amino-bodies.

Amylopsin, the diastatic ferment, has an action on starchy food similar to that of ptyalin, but more rapid and more active, for it can deal with raw starch; the final products are maltose and achroodextrin. The hydrolytic action of amylopsin stops at maltose and achroodextrin, but these are in turn attacked by the **maltase** of the succus entericus, and converted into dextrose before absorption. All starchy food which has escaped conversion in the mouth and stomach is also acted upon in the intestines by maltase.

Lipase or **Steapsin** is the fat-splitting ferment of the pancreas; it possesses the remarkable power of breaking up fats into fatty acids and glycerine, and does this with the object of promoting their absorption. We have learned a little of this action in connection with the bile (p. 245), but must look at the matter again in somewhat greater detail. The power of fats to form emulsions is a valuable property in digestion. In the state of emulsion the fat is very finely divided; milk is a secretion in which the fat is typically emulsified. Emulsion can also be brought about by mixing fat with gum, egg-white, and soap solution. The only fat emulsion received by animals as food is when they are young, and it is said that the wall of the stomach of young animals contains a gastric lipase which deals with this. If so, this section of the alimentary canal is of great importance in those animals where the pancreas is functionless in early life; but of this we have no information in herbivora, though it is a natural condition in man. The fat-splitting power of pancreatic lipase is very marked, but, as mentioned at p. 245, is greatly increased by admixture with bile. When fats are split the fatty acids unite with the alkali of the intestinal and pancreatic secretion, and form soaps. We have seen the action of the combined bile and lecithin in dissolving fatty acids and soaps, and the physiological importance of this, for until solution is effected absorption is impossible. Without the assistance of bile no solution of fatty acids and soaps would occur as the result of the action of lipase.

As free fatty acids, soaps, and glycerine, the fat enters the villus and gains the chyle vessel. At one time it was believed fat in fine emulsion passed between the epithelial cells of the villus, but this is now known to be wrong. The oil globules seen in the villus represent the newly reconstructed fat, for the soluble products of fatty acids, soaps, and glycerine have no sooner got into the villus than neutral fat is reconstructed. Some think this is brought about by the *reversible action* of lipase, others believe the effect is due to the living cells of the villus, and not the result of the action of a ferment. No further change occurs to the fat until it reaches the blood. Oil globules in the blood would not pass along the capillaries, and plugging of the vessels would occur. This is prevented by a change brought about in the blood, by which the fat is rendered soluble, dialysable, and capable of passing through the capillary wall. The method by which the blood effects this change is unknown; it is said, however, that lipase may be found in the blood, muscles, liver, and other glands, and if so this will account for fat embolism not occurring in the vessels, and also explains why the tissues are able to draw on their body fat as required, for this must be brought into solution before it can pass back into the blood.

Lipase is readily destroyed, so that unless quite fresh it does not do its work in artificial digestions. It is believed that a portion of the lipase is secreted in the inactive condition as a zymogen, or pro-enzyme form, and that this is activated by the action of the bile acids and lecithin. Whether this is so or not, the dependence of the pancreatic secretion on the good will of the bile is a very important matter.

On p. 188 we have alluded to Pawlow's work on the quantity and quality of the gastric juice being regulated by a specific action on the part of the food itself. Similarly, the same observer has shown that the ferment contents of the pancreatic juice are adapted to the character of the food; for example, the lipase is increased by a fat diet. A definite and unchanging diet leads to the formation of a pancreatic juice, which is unable to deal effectively with a sudden change in food. The practical bearing of this in the feeding of animals is far-reaching. As a profession we have recognised for years the disastrous effects of sudden changes in diet; modern science offers the explanation of its action. The whole matter is probably regulated by an internal secretion.

The **Changes occurring in the Cells** of the gland correspond very closely with those described for the salivary secretion.

When a pancreas or lobe of a pancreas has been at rest for some time the cells forming it are rendered very indistinct; the lumen of the alveolus is nearly obliterated by their swollen condition, and the cells are seen crowded with granules ; these are so arranged that the margin presents a clear or fairly clear zone, while within this there is an intensely granular zone (Fig. 83, A). The minute granules filling the cell are the mother-substances of the secretion. When activity commences the granules appear to pass centrally towards the alveolus, leaving the cell comparatively clear excepting that portion immediately abutting on the alveolus, which even in the exhausted condition remains granular. These changes result in the cells becoming distinct and clearly defined, and, moreover, as they have emptied their granular contents into the alveolus as pancreatic secretion, they have consequently become much smaller. The narrow clear zone seen in the resting gland has now become broad, the previously choked alveolus is clearly defined, whilst the nucleus of the cell, which was hidden in the charged condition, can easily be seen in the exhausted gland (Fig. 83, B). These changes have been worked out on the pancreas of the living rabbit by Kühne and Sheridan Lea.

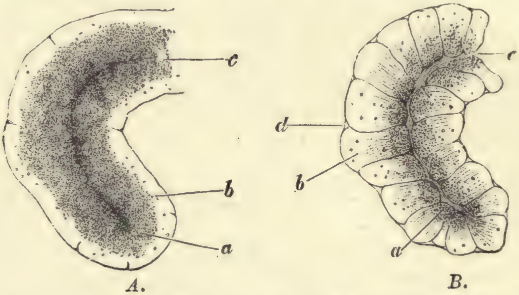


Fig. 83.—A Portion of the Pancreas of the Rabbit (Kühne and Sheridan Lea). A, at Rest ; B, in a State of Activity (Foster).

a, The inner granular zone in A is larger and more closely studded with fine granules than in B, in which the granules are fewer and coarser. *b*, The outer transparent zone is small in A, larger in B, and in the latter marked with faint striæ. *c*, The lumen is very obvious in B, but indistinct in A. *d*, An indentation of the junctions of the cells seen in the active but not in the resting glands.

Amount of Secretion.—From the investigations of Colin and others we know that in most animals the secretion of pancreatic juice is continuous, though not uniform. In ruminants the largest secretion is towards the end of rumination ; in the dog the maximum is reached between the second and fourth hours after feeding, this maximum being followed by a fall, and about the seventh hour by a rise. It will be remembered that the bile gives a similar curve. In the dog it is generally considered there is no secretion during starvation, but immediately food begins to pass out of the stomach the pancreas becomes active. In this connection, however, it is desirable to remember that according to some observers a starved dog will actively secrete pancreatic juice for twenty minutes every two hours. The continuous secretion of the gland in herbivora is provided for by all the lobes not being active at the same time. In the ox the amount of juice secreted is about 265 grammes (9 ounces) per hour, in the horse it is much the same, in the sheep 7 to 8 grammes (¼ to ½ ounce), pig about 5 to 15 grammes (⅛ to ½ ounce) per hour, and in the dog still less, 2 to 3 grammes. There is no necessary ratio between the size of the animal, the weight of the gland, and the amount of pancreatic fluid secreted; carnivora secrete relatively more than herbivora.

The pressure under which the pancreatic juice is secreted is low; it is said to be equal to 18 mm. (0·67 inch) of mercury, which is very little greater than that of the bile.

Pancreatic Diabetes.*—If the pancreas of a dog be completely removed, there is a disappearance of all glycogen from the tissues, sugar appears in the urine within twenty-four hours, and the animal dies in the course of a month or less with diabetes, since the power of oxidising dextrose is lost. The dextrose consequently accumulates in the blood, and is separated by the kidneys. In addition to there being sugar in the urine, there is also an increase in the amount of fluid produced and an excess of urea; consequently there is intense thirst, and this is associated with a large appetite in spite of which the animal wastes. If the depancreated animal be placed on a purely proteid diet, no difference occurs in the amount of sugar excreted; even if no food be given sugar is still formed. If the removal of the gland is incomplete, glycosuria still occurs, but it will vary in intensity from fatal to transient effects, depending upon the amount of pancreas left behind; in fact, it is possible by experience to leave behind just sufficient (one-fourth to one-fifth) of the gland to prevent diabetes arising. In any case, fatal results may be avoided by grafting portions of pancreas beneath the skin, the presence of these preventing diabetes. This proves that the prevention of glycosuria does not depend on the pancreatic juice.

Regulation of the Sugar Supply.—Throughout these remarks on the glycogen question, we have assumed that the view originally put forward by Bernard is correct—namely, that the sugar resulting from the conversion of carbohydrates in the digestive canal is stored in the liver and muscles as glycogen, while a definite proportion of sugar remains in circulation. The chief opponent to this theory is Pavy, who believes that glycogen is never converted back into sugar, but is built up into fat and protein. Further, he denies the existence during life of a liver ferment capable of converting glycogen into glucose. He showed that egg-albumin was capable of being so treated that it yielded a reducing sugar, which was obtained from the carbohydrate group of the protein molecule, and serum globulin behaves similarly; mucin and nucleo-albumin are also now known to contain the same substance. The importance of this discovery was considerable, as the production of sugar from protein, though suspected, had not been proved. The diet of the omnivora and herbivora contains more carbohydrate than can be accounted for in the muscles and liver as glycogen, and it is certain that all over and above that required for the purposes of sugar must be converted into fat, and some of it incorporated with the protein tissues. Nevertheless the Bernard doctrine explains why the percentage of sugar in the circulating blood is constant—viz., by the gradual doling out of glycogen as sugar from the liver under the influence of a ferment in that gland, and physiologists have, with but few exceptions, accepted his teachings.

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* To avoid repetition, this matter should be read in conjunction with the remarks on Glycogen, p. 246.

What we have now to consider is the manner in which this regulation is effected. The first to throw some light on the process was Bernard, who showed that if the floor of the fourth ventricle be punctured temporary diabetes results, sugar appearing in the urine, while the liver uses up its glycogen. The spot in the medulla is known as the diabetic centre, and the puncture acts, not by destroying, but by stimulating its activity. This is proved by the fact that if the animal be starved before the puncture is made no sugar appears in the urine, as no glycogen exists in the liver. The nerves passing to this centre—the afferent nerves—are contained in most of the sensory nerves of the body; if these are stimulated they act reflexly on the diabetic centre, and sugar in the urine results. The same occurs on stimulating the cerebral end of the divided vagus. The impulses from the diabetic centre to the liver pass down the spinal cord, and emerge in the anterior thoracic region with the inferior roots of the spinal nerves, and are connected with the inferior cervical and thoracic ganglia by the *rami communicantes*; from these ganglia the impulses pass by means of the splanchnic nerve to the liver. Whether the splanchnic contains fibres which secrete the ferment is unknown, but stimulation of the inferior cervical and thoracic ganglia produces glycosuria provided the splanchnic remains uncut. At one time it was considered that these results were due to vasomotor effect, and that vascular dilatation, rather than secretory activity, was brought about by stimulating the splanchnic, but it is now known that glycosuria is produced when the central end of the depressor nerve is stimulated, and the effect of stimulating this nerve is to cause a fall in abdominal blood-pressure. The impulses passing to the diabetic centre may, it has been suggested, originate in the contracting skeletal muscles by the compression of the muscle spindles. The heart muscle contains more glycogen than skeletal muscle; when the amount of glycogen in the latter has fallen to one-tenth or even one-thirtieth of the normal the heart muscle still maintains its due proportion. The fibres from the heart to the diabetic centre are conveyed in the vagus, and it is easy to see that on this theory the heart, which is the most active muscle in the body, may regulate the production of the material which furnishes it with energy.

In distinction to the above, which may be termed the 'nervous theory of sugar liberation,' we have another, the chemical, based upon the knowledge which exists of the glycosuria, which results from depriving an animal of its pancreas. In some way or other which is not known, the pancreatic tissue is intimately mixed up with the sugar question, and this can be explained on the supposition of an *internal secretion*, which prevents the blood from becoming overloaded with sugar, either by regulating the amount which is liberated from the liver, or by stimulating the sugar-splitting action of the tissue-cells. It would on this basis be reasonable to suppose that the pancreatic extract should yield a glycolytic substance, but no such has been found. That the visible pancreatic secretion takes no share in the process is evident from what has been previously stated—viz., that if only a fragment of pancreas is left behind in the body of a depancreated animal no glycosuria results.

An extract of pancreas, it has been stated above, has no glycolytic power; further, an extract of muscle has no sugar-destroying power, but if the extracts be mixed glycolysis results. From this it has been supposed that the pancreatic extract activates a sugar-destroying enzyme present in muscle, which enables the latter, under physiological conditions, to oxidise sugar in the body, and obtain from it heat and energy. The activating substance furnished by the pancreatic extract is not an enzyme, for if the extract be boiled the substance is not destroyed; it is therefore assumed that the internal secretion of the pancreas is a *hormone* (see p. 230). There are others who consider that the function of the internal secretion is not to furnish the tissues with the power to metabolise sugar, but rather that it regulates its output from the liver, and that when this regulation fails diabetes results, owing to the excess of sugar in the blood. The balance of evidence, however, suggests that the difficulty lies with the tissues—especially the muscular—being unable to oxidise the sugar brought to them.

The pancreas in structure resembles the salivary glands, in being compound tubular, but in it may be seen with the naked eye spherical or oval bodies, which are obviously not ordinary pancreatic tissue; these are known as the *Islands of Langerhans*. The islands are composed of a group of cells surrounded by a rich capillary network of bloodvessels, and the view has been advanced that they are the seat of the production of the internal secretion. Ligature of the pancreatic duct causes the ordinary gland tissue to atrophy, but does not affect the islands, nor does ligature produce glycosuria. This is evidence in favour of their furnishing the internal secretion, but there are other observers who consider the islands are connected with the ordinary pancreatic secretion.

Diabetes.—In the forms of glycosuria hitherto dealt with, its production has been experimental. But there is a pathological condition in which much the same symptoms are present, and though, so far as we know, the herbivora do not suffer from this disease, it has been described in the dog, and under any circumstances its features in man are of interest to us. In diabetes the sugar in the blood, instead of being 0·1 per cent., as it normally is in man, may rise to 0·4, or even as high as 0·7 or 1 per cent. In consequence of the tissues being unable to consume the dextrose brought to them, the sugar passes off by the urine, and the body is starved of its source of heat and energy. As the disease advances, not only sugar, but products of deranged protein and fat metabolism, appear in the urine, such as *acetone*, *aceto-acetic acid*, and *oxybutyric* acids. These acids, by combining with the alkali of the blood, reduce the carbon dioxide carrying capacity of the fluid, and, in consequence, the carbon dioxide accumulates in the tissues, and *diabetic coma* results.

Pathological.

The most common pathological condition of the liver is **Jaundice**, and the majority, if not all, cases of jaundice are obstructive—viz., there is some obstruction to the free pouring out of bile; in consequence there is a backward pressure, which being greater than the low blood-pressure under which bile is secreted, the bile is reabsorbed, and stains the tissues yellow. There is also a form of jaundice affecting the horse and dog in South Africa, due to a parasite in the blood; in these cases the yellow tint is derived from the destruction of red corpuscles stimulating the production of bile (see p. 243). **Biliary Calculi**, consisting largely of cholesterin, are not uncommon in ruminants, but rare in the horse. **Fatty Liver** is common in all animals overfed and underworked. In the horse it may lead to **Rupture** of the liver during work. **Enlargements** of the liver are very common as the result of vascular disturbance elsewhere; it is not uncommon as a sequel to pneumonia, strangles, and other prolonged febrile changes. **Abscess** of the liver is rare, but not unknown. **Parasitic** disease of the liver is one of the epizootic diseases of sheep, and common in the ox, but rare in the horse. The parasite occupies the bile-ducts, which become practically occluded.

In India, calcareous degeneration of the liver is one of the most common affections of this organ, and throughout the tropics generally liver disorders are very frequent.

The pancreas is seldom the seat of pathological disturbances ; it may be affected with abscess in strangles or in septic diseases, but such conditions are unrecognisable during life.

Sugar in urine is described as occurring in dogs ; we have never met with it in horses, though *polyuria* is a common affection.

CHAPTER VII

ABSORPTION

SECTION I.

Lymph.

LYMPH may be regarded as the material by which the tissues are directly nourished, and by which effete material is collected from them and taken back to the blood ; there are certain non-vascular structures, such as the cornea, cartilage, etc., where the lymph circulation is the only means by which the part is supplied with nourishment. Speaking generally, the lymphatic system may be described as the drainage system of the body, in contradistinction to the blood or irrigating system. Though the latter is not exclusively devoted to irrigating, it may also take up material from the tissue spaces.

The Lymph Spaces.—The tissues are bathed in lymph, which is contained in the lymphatic spaces existing between the capillary bloodvessels and capillary lymph-vessels. There is a constant passage of material from the blood into the tissues, from the tissues into the lymph, and likewise from the tissues back to the blood.

The lymph spaces are irregular passages in the connective tissue, the larger ones being lined by epithelioid plates of a peculiar irregular outline ; these spaces exist outside the bloodvessels, and the lymph finds its way from the bloodvessels into the lymph spaces. From the lymph spaces the fluid reaches the lymph capillaries, but the means by which it gets there is not clear, for it appears certain that, excepting in a few cases, there is no direct communication between the space and the capillary. In the vessels of the brain a peculiar arrangement is present ; the lymphatic vessel surrounds the artery, and obtains its lymph direct ; these are known as perivascular lymphatics. The lining of the **Lymph Capillary** is composed of the same epithelioid plates with irregular outline which are found in the spaces, and it is believed that at the junction of the plates, crevices or intervals may exist through which fluid may find its way by the simple process of transudation. From the lymph capillary begins the **Lymphatic Vessel,** which, in addition to an epithelioid lining, has also a muscular coat, more marked in the large than in the small vessels, and also a connective-tissue covering. In the interior of these vessels valves are found which are essentially similar in structure, arrangement, and mode of action to those in the veins. Immediately beyond each valve there is a dilatation of the vessels which gives them a beaded appearance when the lymphatic is distended.

The whole of the lymphatics of the body converge towards a central vessel, the thoracic duct ; those from the left side of the head and neck, the left fore-limb, the chest, abdominal cavity, and hind-limbs, unite with the duct at different points, and this in turn opens into the anterior vena cava ; from the right side of the head and neck, and right fore-limb, the vessels collect and pour their contents by a separate duct into the same vein. The thoracic duct is nothing more than a large lymphatic vessel, possessing the same structure as the lymphatic vessels above described, the muscular coat being especially well marked. The thoracic duct receives the lymph, not only from the ordinary tissues, but also from the intestinal canal. During starvation the mesenteric lacteal vessels convey to the duct a fluid which is essentially lymph, but during digestion this clear fluid is replaced by a turbid white fluid known as chyle ; at this period the lacteal vessels are carrying not only lymph, but also the products of digestion, the milkiness of the chyle being due to the presence of emulsified fats.

The **Serous Cavities** of the pleura, pericardium, and peritoneum, have been looked upon as large lymphatic spaces, though this is now considered doubtful. The fluid they contain is lymph, and they are in direct communication with lymphatic vessels, especially those of the diaphragm. In the diaphragm slits or stomata exist, and into these the lymph readily finds its way, being aspirated into the vessels during the respiratory movements of this organ ; so readily is this effected that the diaphragm may be injected in a recently dead subject, by placing some milk on its surface and establishing artificial respiration.

The lymphatic vessels in their course pass through bodies known as **Lymphatic Glands,** entering at one side and emerging at the other. Experience shows that in its passage through these glands the lymph has corpuscles added to it which ultimately become white blood-corpuscles, and, moreover, it acquires the property of clotting. The gland consists of a *capsule*, within which is a mass of adenoid tissue divisible into a *cortex* and *medulla.* The capsule sends in bands of tissue (*trabeculæ*) which divide the gland into compartments or *alveoli,* those in the cortex being much larger than those in the medulla. The alveoli contain a network of connective tissue, whose central part is finely meshed (*adenoid tissue*), closely packed with lymph corpuscles, and constitutes the *glandular substance.* The adenoid tissue does not occupy the entire alveolus, but fills up the centre, and is maintained in position by branched, nucleated, connective tissue corpuscles passing to the wall of the alveolus. In this way a space or channel is formed between the central mass of adenoid tissue and the wall of the alveolus; this channel is known as a *lymph sinus* (see Fig. 84). It is through the lymph sinuses of

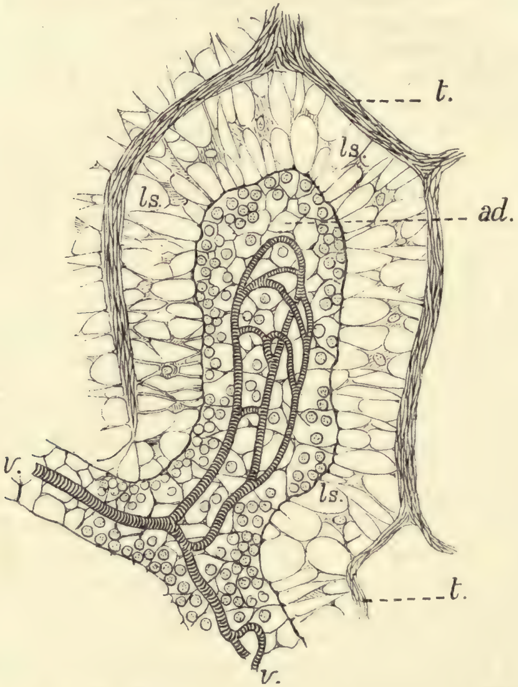


FIG. 84.—DIAGRAMMATIC SECTION OF LYMPHATIC GLAND.

ad, Adenoid tissue containing lymph corpuscles. The region *ad* is normally densely packed with lymph corpuscles, and constitutes the glandular substance. The corpuscles are here drawn in scanty numbers, so as not to obscure the central capillary *v.* In the adenoid tissue may be seen a capillary bloodvessel *v.* Outside the core of adenoid tissue is the lymph sinus or space *ls,* across which run branched nucleated corpuscles which are simply an open network of connective tissue. Surrounding the whole is the trabecular framework *t.*

the cortex that the gland is in direct communication with the afferent lymphatic vessels. In the adenoid tissue of the alveolus there is a network of bloodvessels ; the tissue itself is filled with corpuscles known as leucocytes, which are also found in the more open network extending across the lymph sinus. The medulla of the gland presents no essential difference in structure to that of the cortex, excepting that the reticular network is more complex, closer, and more extensive. The efferent lymphatic vessels originate in the lymph sinuses of the medulla.

Lymph is a slightly yellow-coloured fluid, alkaline in reaction, with a specific gravity of 1012 to 1022, and possessing the power of spontaneous clotting. The clot it yields is not so firm as that of blood, and takes longer to form ; moreover, the bulk of fibrin is much smaller. Lymph may be regarded essentially as blood minus the red corpuscles ; it contains, therefore, the proteins of that fluid—viz., fibrinogen, paraglobulin, and serum albumin, though in smaller amounts, also cells resembling the white cells of the blood, extractives, salts, and gases. The fluid in which these are contained is spoken of as lymph plasma. The gases consist principally of carbon dioxide, the amount of which is greater than in arterial, but less than in venous blood, a small quantity of nitrogen, and only traces of oxygen. Amongst the extractives some observers have found urea, a substance which exists more largely in lymph than in blood, and which is said to be always present in the cow. The salts are distributed much as are those in blood—viz., potash in the corpuscles, and soda in the plasma. It is evident that the composition of the lymph cannot be uniform, but must depend, among other causes, upon the nature of the food-supply and the source of the lymph.

The lymph-cells or leucocytes exhibit amœboid movements, and are identical with white blood-cells ; they are more numerous in those vessels which have passed through lymphatic glands, for it is in the gland that the leucocytes are manufactured and added to the lymph. The cells consist of proteins, lecithin, cholesterin, and fat, and their nuclei contain nuclein. Owing to their power of movement, they are able to pass through the bloodvessels into the tissues, and *vice versa*. The proportion of lymph corpuscles to fluid is about the same as the proportion of white corpuscles to blood.

The Quantity of Lymph in the Body is difficult to determine, and varies considerably. From a lymphatic vessel in the neck of the horse Colin obtained ½ to 2 kilogrammes (17 to 70 ounces) in twenty-four hours ; but the variations were wide. Colin noticed that the herbivora secrete more lymph than the carnivora, and young animals more than adults. From the thoracic duct of a cow this observer obtained the prodigious quantity of 91 kilogrammes (20 gallons) in twenty-four hours. This, of course, is no guide to the amount of lymph in the body, as the thoracic duct is a mixture of body lymph and chyle from the intestines. In the observation mentioned on the cow the amount of material collected from the duct was more than double the blood in the body; and if, as is usual, we regard two-thirds of the contents of the thoracic duct flow to represent chyle and one-third lymph, it still leaves the lymph flow at a very high figure—in fact, nearly equalling the entire blood-content of the body. As a matter of fact, the total lymph in the body is unknown; it has been supposed that it may be two, or even three, times greater than that of the blood.

In the following table from Colin the amount of mixed chyle and lymph flowing from the thoracic duct was measured; the minimum represents a period of comparative digestive quiescence; the maximum amounts represent digestive activity.

Horse	- 14 to 40	kilogrammes	(24 to 70 pints) in 24 hours.
Ox	- 20 to 91	,,	(35 to 160 pints) in 24 hours.
Sheep	- 3 to 9·5	,,	(5 to 16 pints) in 24 hours.
Dog	- 1·3 to 2·6	,,	(2½ to 4½ pints) in 24 hours.

Formation of Lymph.—The method by which lymph is formed has been the subject of great difference of opinion and innumerable experiments. The question is still unsettled, so that it is necessary to present both views of the case. The difficulty in explaining the production of lymph lies in the fact that the blood system and lymph system of vessels do not communicate; both, in fact, are closed systems, while between them lies the tissue spaces. What has to be explained is the passage of fluid from one to the other across this space. If secretory nerves had a definite existence in lymph production, all difficulties would disappear; but though these have been suspected, and by some even described as existing, the balance of evidence is against their presence. But even quite apart from the existence of a special nervous mechanism, there are other grounds on which the theory of lymph formation could easily be explained—viz., on a physical basis, as of filtration, or diffusion; but, unfortunately, these frequently fail, under experimental inquiry, to behave in the living body as they do in the dead cell, though, in spite of this, physical processes have been, and continue to be, invoked as an explanation in those cases where their action is not negatived by experimental methods. Finally, the explanation of the selective action of the living tissue-cells has been urged as the real explanation of the phenomenon. As a matter of fact, it is no explanation, though it may, and probably does, tell us something of what is occurring, or fixes on the means by which it is taking place. Nevertheless, if the cell could be proved to be the factor in lymph formation, it would make a substantial addition to our knowledge of the subject ; the difficulty of explaining the selective power of the cell which secretes lymph is only the same difficulty which exists in considering the cell which secretes urine, or bile, or sweat. Neglecting entirely the nervous mechanism, of which there is so little evidence, the two chief theories of lymph formation resolve themselves into the physical and secretory, and each of these must be examined separately.

The **Physical Theory** is based upon a knowledge of the laws governing filtration, diffusion, and osmosis, and were first employed by Ludwig.

Two liquids miscible, but utterly unlike, if brought into contact will gradually form a homogeneous mixture as the result of diffusion. If they be separated by a membrane permeable to their molecules, diffusion will occur through this, and a mixture of uniform composition result. Diffusion through a membrane is known as osmosis. Substances which are diffusible are known as crystalloids, those which are non-diffusible are called colloids. Sugar or salt are good examples of diffusible bodies, proteins and starch are examples of colloids, the large size of the molecules of the latter preventing their passage through an animal or other membrane. This difference in the behaviour of these two classes of substance as regards their osmotic properties, affords a useful and ready means, known as *dialysis*, of separating the crystalloids from the *colloids*.

If two masses of water be separated by a membrane the diffusibility of each being equal, as many molecules will pass into one chamber as enter into the opposite, though to all appearances no change in the fluid is taking place. If one chamber contains salt solution and the other plain water, it will be found that much more water passes into the salt solution than salt solution into the water, the rate of transference of the salt depending upon the concentration of the salt solution ; the force which brings this about is known as the *osmotic pressure*. It can be shown that the osmotic pressure is proportional to the number of molecules of the crystalloid in solution.

Filtration is the passage of fluid through a membrane as the result of pressure. If the pressure of blood in the capillaries could be shown to be higher than the pressure in the lymph vessels or spaces, adequate ground would exist for regarding filtration as an agent in lymph production. As a matter of fact, the pressure in the lymph spaces is unknown, the pressure in the lymph capillaries is unknown ; but there is the best of reason for believing that the pressure falls from the blood capillaries to the lymph capillaries, and by increasing the pressure in the former—say, by tying or compressing a vein—œdema results in consequence of the filtration of fluid from blood capillary to tissue space. The fluid in the tissue space may or may not be lymph as we find it in a lymphatic vessel. The plasma has passed through the wall of one vessel and become altered in composition; in the tissue space it is certain that further change in its composition occurs in consequence of tissue activity, and another vessel wall has to be negotiated before the lymph-stream is reached; this passage may occasion further change in its nature. The question of the actual changes in the composition of the lymph in its passage from blood capillary to lymph capillary does not immediately concern us here, but it helps to explain why some physiologists have such difficulty in accepting purely physical reasoning where living tissues are concerned, even when the process concerned is as simple as that of filtration. Nor must it be considered that the presence of an increase of pressure in the capillaries necessarily results in the formation of more lymph. In the horse it has been shown that the flow of lymph from the parotid gland is not appreciably increased when the gland passes from a condition of rest to that of secretory activity, and yet we know that the capillary pressure at the time is greatly increased. Other evidence will be quoted later showing that serum may be absorbed from the bowel when the pressure in the capillaries is greater than the pressure in the intestines; it may be urged that the case of the bowel and bloodvessel is not comparable with that of the tissue space and bloodvessel, but the object is rather to show that filtration may be non-existent at the moment when the necessary physical conditions for its activity are present. It has been shown, therefore, that there are features in lymph formation which cannot be entirely explained on the theory of filtration.

Diffusion and Osmosis.—For many years it has been known that if two fluids—one containing salt, and the other pure water—be separated by a membrane of parchment, one passes into the other through the pores of the membrane, until the same amount of salt exists on both sides of the diaphragm. Fluids which thus pass through are termed **crystalloids**; those which refuse to pass through are known as **colloids**; while the entire process is termed **osmosis** or **dialysis**. We shall see presently that physical chemistry of the present day gives a more restricted definition to the term 'osmosis.'

It is known that perfectly pure water is not a conductor of electricity, and the same may be said of solutions of sugar, urea, albumin, and other bodies. The explanation afforded by modern chemistry is that the molecules of pure water and molecules of sugar undergo no *dissociation* into their constituent *ions*. Substances which dissolve in water and undergo dissociation are conductors of electricity. For instance, sodium chloride is broken up in water into sodium *ions* and chlorine *ions*, each group being charged with an opposite form of electricity, the sodium ions being positively, the chlorine ions negatively, charged.

Substances so capable of dissociation are termed *electrolytes*, and their interest to us at the present time is in connection with osmosis; the act of dissociation liberates a number of ions, and by so doing increases the number of particles moving in the fluid. It can be shown that osmotic pressure—a term yet to be explained—is proportional to the number of molecules of dissolved substances present, and in the above example the ion behaves as a molecule in osmotic pressure. Generally speaking, the greater the dilution, the larger the number of ions dissociated.

Though not directly connected with the matter under consideration, it is convenient in this place to look at the part played in the body by *ionic* action. Thus it is possible that the contractile tissues which work in a saline artificial circulation (p. 49) are capable of so doing in consequence of a due adjustment of ions in their surroundings; and the same may be said of cilia, amœboid action, and such-like, each requiring its own definite proportion of ions. Loeb has classified the ions responsible for rhythmic contractions, though such a classification can at present only be regarded as provisional. So much importance does this observer attach to ionic action that he has brought forward evidence to show that fertilisation of the ovum may be ionic in its nature, the spermatozoa merely regulating the proportion of ions. Even a nerve impulse he regards as depending on an electrolytic action.

Osmotic Pressure.—If a solution of an electrolyte such as common salt be enclosed in a specially prepared semi-permeable cell, water will pass in, but salt will not pass out, either by filtration or diffusion. This can be ascertained by placing the cell in distilled water, and if a manometer be connected with the cell it will be found that as the water passes in the pressure increases. This pressure is known as osmotic pressure, and the term 'osmosis' at the present day is confined to the stream of water passing through a membrane, while dialysis is restricted to the passage of the molecules dissolved in water. If in the above experiment the solution of salt was 1 per cent., it will be found that, if the strength be doubled, the manometer will indicate twice the pressure, so that the amount of osmotic pressure is always proportional to the number of molecules of the dissolved substance in a given volume of the solution.

The nature of osmotic pressure is unknown; it can be shown to be independent of the nature of the substance in solution, and proportional to the number of molecules of the dissolved substance. It is governed by laws closely analogous to those governing gaseous pressure, and, as in the case of gases, it is affected by variations of temperature and by the law of partial pressure. The latter, in the case of osmotic pressure, is expressed by saying that the osmotic pressure of a solution of different substances is equal to the sum of the pressure which the individual substances would exert if they were alone in the solution. Osmotic pressure is conveniently estimated by ascertaining the freezing-point of a substance soluble in water, which is always lower than that of the water itself; the lowering of the freezing-point is proportional to the molecular concentration of the dissolved substance, and this molecular concentration is proportional to osmotic pressure. Sugar, for instance, not being an electrolyte, has a smaller number of particles moving in the solution than sodium chloride, which is capable of dissociation, so that the osmotic pressure of salt is higher than that of sugar. A 1 per cent. solution of sugar has an osmotic pressure of 473 mm. mercury, while 0·9 per cent. of common salt which has the same osmotic pressure as blood-serum exerts a pressure of 5,000 mm. mercury.

Blood-serum is taken as the standard in physiological inquiry; any solution which has the same molecular concentration as serum, and consequently exerts the same osmotic pressure, is termed **isotonic**; if it has a greater osmotic pressure, it is termed **hypertonic**; and if less, **hypotonic.** For example, on p. 6 the action of salt solution on red corpuscles has been described; if the addition of a solution causes no effect, it may be known that it is isotonic to the material within the corpuscles; if it causes the corpuscles to shrink and become crenated, it has a greater osmotic pressure than the cells, and is hypertonic; if it causes them to swell and discharge their pigment, it has a smaller osmotic pressure, and is hypotonic.

It is not difficult to see how the physical factors of osmotic pressure and diffusion may be turned to account in explaining the formation of lymph, absorption from the intestines, secretion of urine, and such-like processes. The danger, as has been previously indicated, lies in their uncompromising application, and in the liability to forget that the living body is neither a parchment membrane nor a vessel with a semi-permeable lining. It has been urged that it is impossible to disregard the value of osmotic currents in restoring equilibrium of composition between the blood and the tissues or the tissues and the blood; for example, if a strong solution of common salt be injected into the blood-stream, a current is created from the tissues into the blood, by which the tissues may lose water; but later on diffusion will come into play, and the tissues will draw water from the blood. It is suggested that constant and rapid osmotic changes are occurring between the blood and the tissues; so rapid, indeed, may these be that if the osmotic equilibrium be upset by injecting a large dose of dextrose, within half a minute it is readjusted, We have seen that the lymph in the spaces must necessarily be undergoing constant change in its composition and concentration, as the result of tissue activity, with its attendant chemical changes; and it is readily conceivable that osmotic or diffusion currents may be set up, water being drawn from the blood to the tissue spaces, and crystalloid bodies, such as would result from the breaking up of the protein molecule, passing by diffusion from tissue spaces to blood, and so being got rid of by the excretory organs, of which the precursors of urea are a good example.

Experimental inquiry, however, shows that it is not easy to explain lymph formation by osmosis or diffusion, and we have previously seen how far filtration has failed. The injection into a vein of a strong solution of common salt, urea, or dextrose, is followed by an immediate *increase* in lymph; whereas the osmotic pressure exerted by sodium chloride, for example, should diminish the secretion by setting up osmotic currents from tissues to bloodvessel. Even as regards absorption, which it is difficult to divorce from lymph formation, osmotic pressure does not help as much as might be expected. Experimentally it can be shown that there is no definite relation between the rate at which the sugars are absorbed and the osmotic pressure they exert. Serum, isotonic with blood plasma, may be absorbed from a loop of intestine, when the blood pressure in the capillaries of the intestine is greater than the pressure within the bowel. Evidently in this case osmotic pressure cannot have been exercised, while absorption by filtration is negatived by the higher pressure in the capillaries. Salt solution isotonic with blood plasma may also be readily absorbed by the bloodvessels in the peritoneal cavity. In all these cases something is occurring which is opposed to what might have been expected on a purely physical basis. But perhaps few things are more remarkable in this respect, or more difficult to explain, than the effect of the injection of dextrose, which causes a *post-mortem flow of lymph* for as long as an hour after the circulation has ceased. Whether the question be considered from its physical or secretory aspect, this post-mortem flow is inexplicable.

Indiffusible substances such as protein are believed to exert but little osmotic pressure, and some consider none whatever. The large size of the protein molecule, and the small number present in such concentration (as 6 or 7 per cent.), as is represented by blood serum, explains why they exert little or no pressure. The passage of protein through the capillary wall to the lymph vessel cannot be satisfactorily explained by osmotic pressure ; a filtration has consequently been assumed to be the agent at work, as the blood in the capillaries is at a higher pressure than the lymph in their capillaries.

Starling, whose name is so closely identified with the investigation of lymph production from its physical aspect, has urged the permeability of the capillary wall as an important factor. His observations show that the normal undamaged capillary of the limbs and connective tissue offers a very considerable resistance to the filtration of lymph, and keeps back a large portion of the proteins of the blood plasma ; on the other hand, the intestinal capillaries, and especially the capillaries of the liver, are very permeable ; a very small capillary pressure in the latter suffices to produce a large transudation of lymph containing as much protein as the plasma itself. A capillary of a limb normally impermeable may by injury be at once converted into a permeable capillary, within which the slightest increase in pressure brings about lymph production.

Starling records the remarkable fact that no lymph can be obtained from a *resting* limb, though active or passive movements of it at once cause a flow of lymph. The only part of the body which produces a continuous flow of lymph during rest is the alimentary canal. Though no lymph is yielded by a resting limb, yet the chemical changes in the tissue are still occurring, oxygen is being absorbed, carbonic acid and other waste products got rid of, but their channel of excretion is effected by the blood-vessels.

The Secretory Theory of lymph formation is based on a knowledge of the secretory activity of epithelium in general. It was natural to regard the endothelial lining of the capillary vessels as the possible seat of secretory activity, as was known to be the case in other tissues; and when Heidenhain was able to show that by the injection of certain substances into the blood he was able to increase the flow of lymph without increasing the arterial pressure, it appeared that the solution of the vexed question of lymph formation was at hand.

Heidenhain found that the injection into the blood of peptone, extracts of leech, crayfish, muscle, egg-albumin, etc., increased the rate of lymph flow, and also the total solids in the lymph obtained from the thoracic duct. He called these substances **lymphagogues,** and divided them into two classes, the first class being the above, while the second consisted mainly of crystalloid bodies such as sugar and salt, which, though increasing the total bulk of lymph produced, rendered it more watery than usual.

Regarding Class 1, Heidenhain believed they contained a specific substance which stimulated secretion. Starling showed that the increased secretion was derived from the liver; he believed the extracts acted pathologically on the walls of the blood capillaries of the gland, and rendered them more permeable; hence the increased flow of lymph. The second class of lymphagogues was believed by Heidenhain to act by attracting water from the tissues, and hence increasing the bulk of lymph. Starling, however, maintains in this case that they act by increasing the osmotic pressure of the circulation, so that water is attracted from lymph and tissues into the blood by osmosis. The excess of fluid thus produced in the blood causes a rise in the capillary pressure, especially that of the abdominal area, followed by increased transudation from the capillaries into the lymph-vessels.

At present it is not possible to decide between the rival theories of lymph formation; it may be proved that under given conditions both play a part in the process. It seems impossible to exclude the living activity of the cell-body, so strongly urged in the matter of other secretions, while it is equally certain that there are other conditions which are only possible of explanation on a physical basis.

The **Movement of Lymph** is largely brought about by muscular contractions in the neighbourhood of the vessels, by which means they are compressed and their contents forced onwards, since the valves which the vessels contain prevent a back flow. The obstruction caused by the lymphatics passing through glands is not serious, while the involuntary muscle fibres in the capsule of the gland more than compensate by their contraction for any resistance in the gland itself. The pressure of the lymph in the lymph-vessel is higher than that in the jugular vein, so the flow of lymph from the tissues to the vein is assisted by the fact that the fluid is passing from a region of higher to one of lower pressure. The movements of the diaphragm, tendons, and fasciæ produce an aspirating effect on the lymph circulating through them. In the case of the diaphragm the lymphatic vessels drain the two large lymphatic sacs, the pleura and peritoneum; owing to the direction taken by the fibres of the diaphragm, compression is exerted on the lymph spaces during its contraction, while a sucking action is produced when it relaxes. This pumping arrangement exists in tendons, fasciæ of muscles, etc., and is a valuable aid in lymph circulation. In the ordinary skeletal muscles during contraction the lymph is squeezed out of the part by compression. During rest practically no lymph passes by the lymph-vessels of muscle, the exchange taking place, as we have seen, by the bloodvessels.

Once the lymph from the abdominal viscera and hind-quarters has found its way into the thoracic duct, its passage into the general circulation is favoured by gravity, by the muscular contraction of the coats of the duct, and by movements of the skeletal muscles, especially the abdominal. The lymph from the right side of the face, neck, and right thorax has a duct of its own, and this is so situated that gravity plays an important part in moving its contents along. Both the thoracic duct and the right lymphatic duct empty into the veins near the heart, either the anterior vena cava or the jugular confluent. The mode of entry varies; in fact, there are great variations in animals of the same species, in the anatomical arrangements, not only of the ducts, but also of their terminations; for example, the thoracic duct is frequently duplicated in the ox.

In whatever way connection with the venous system is made, a valvular arrangement, looking towards the vein, exists between the dilated termination of the lymph-duct and the bloodvessels intended to prevent a reflux of blood into the duct. This valvular seal is a reliable one in the ruminant; in the carnivora it is less so; in the horse it is imperfect, so much so that blood may find its way even for some distance into the duct, and stain the contents, as first pointed out by Colin. If a manometer tube be placed in the thoracic duct of the ox at its termination in the vein, the mixed contents of chyle and lymph will rise in the tube, and in about five minutes reach a maximum. The amount of this is variable; Colin has registered during full digestion a 3-foot pressure (say 75 mm. mercury) in the thoracic duct, which is about one-third of the aortic pressure. This is very high—indeed, is higher than that of the blood in the capillaries or of lymph in the lymph-vessels. It would appear that this marked degree of pressure can only be due to contraction of the walls of the *receptaculum chyli* and contraction of skeletal muscles, the abdominal muscles doubtless taking the largest share. The fluid in the tube rises and falls, and if the tube be removed lymph issues from the vessel in jets. The rise and fall of level in the tube is associated with respiratory movements, but the effect produced is not the same as the general effect caused by inspiration and expiration on blood pressure. Inspiration does not, for instance, draw the lymph from the duct towards the vein—its effect is the reverse; while expiration, on the other hand, raises the pressure in the duct, and discharges its contents. Colin, who first described this singular fact, explains it by saying that the intrathoracic pressure being reduced during inspiration, the vessel dilates, and, in consequence, its capacity is increased. During inspiration it fills up, while at expiration the pressure exercised upon it, no doubt particularly by the abdominal muscles during expiration, causes the now distended duct to discharge its contents. Colin, in fact, observed that the oscillations of the fluid in the manometer tube are greater during laboured respiration. In the horse the pressure in the thoracic duct must be much less than in the duct of the ox; in fact, for blood to pass into the duct the pressure must be at times below that of the pressure in the anterior vena cava. There are great experimental difficulties in getting at the duct in the horse, and exact information is wanting.

As fast as the lymph finds its way from the bloodvessels into the spaces it is normally passed on to the lymphatic capillaries, so that the rate of output is equivalent to the rate of removal; when, however, the output is greater than the rate of removal the lymph accumulates in the tissues, and **Œdema** results. It is conceivable that the rate of removal need not necessarily always be at fault, but that the rate of secretion may be so greatly increased that the outgoing channels are unequal to the demands made upon them. Such an increased secretion of lymph lies on the shoulders of the vascular system, and experience shows that in the majority of cases increased formation of lymph is a more common cause of œdema than defective drainage. It is well known that interference with the venous circulation is productive of œdema, the explanation being that there is not only an increase of pressure in the capillaries as the result of the venous obstruction, but also the venous blood is kept in contact with the wall of the capillary, and this induces changes in the epithelioid cells resulting in increased lymph formation. The swollen legs so common in horses kept idle in the stable are due to this cause. The venous blood ascends the limbs against gravity, and exerts on the capillaries of the legs below the knees and hock a pressure which is nearly equivalent to the height of the vein ; as a result, the cells of the capillary wall are the seat of an increased exudation, and the legs accordingly ' fill,' a condition at once removable by exercise. The pressure in a lymph-vessel is low ; in the neck of the horse it was found to be from ½ to ¾ inch of a weak solution of soda ; in the dog the lateral pressure was half that found in the horse.

The lymph moves slowly in its vessels. Weiss has observed a rate of from 230 to 280 mm. (9 to 11 inches) per minute in a large lymphatic in the neck of the horse, but the velocity in the small vessels is very much less. Colin observed 120 mm. (4¾ inches) per minute. The flow from the thoracic duct of a calf was found by Colin to be 1 metre (3 feet 3 inches) a minute ; in a large mesenteric vessel the same observer found the velocity to be 840 mm. (33 inches) a minute.

SECTION 2.

Chyle.

In the thoracic duct the lymph from the body meets with the lymph coming from the intestines, termed 'chyle.' This chyle is derived from the villi, and passes up the mesentery by many vessels, which in the horse are said by Colin to number 1,200. Each of these passes through a lymphatic gland before entering the *receptaculum chyli.* Chyle is closely allied to lymph in its chemical composition, but it differs from it in containing, during digestion, a quantity of neutral fat, which gives it a milky appearance. The amount of this fat in dogs may vary from 2 per cent. to 15 per cent., or even more. The fat is partly in the condition of measurably large droplets, such as are seen in milk, but the bulk of it exists as extraordinarily minute particles; hence the name 'molecular basis,' which is applied to the fat particles in chyle collectively.

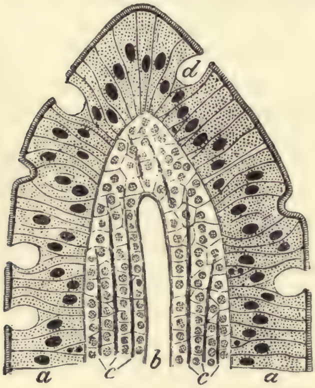
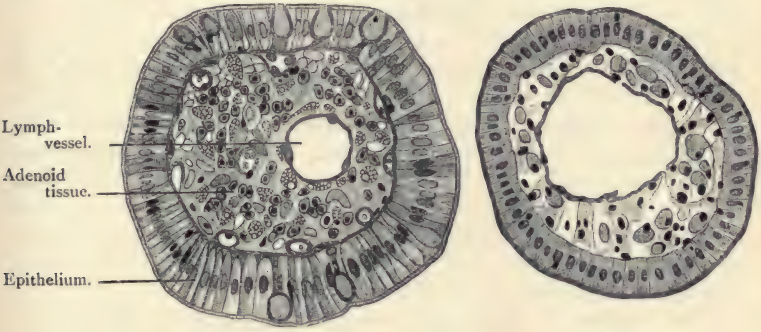


FIG. 85.—VERTICAL SECTION OF A VILLUS: CAT. × 300 (STEWART).

a, Layer of columnar epithelium covering the villus — the outer edge of the cells is striated; *b*, central lacteal of villus; *c*, unstriped muscular fibres; *d*, mucin forming goblet cells.

The Villi.—We have mentioned that in the ordinary tissues the radicles of the lymph vessels are the lymph spaces, but in the wall of the small intestines the origins of the lymph vessels are highly differentiated structures, known as villi and solitary glands. The villi (Fig. 85) are innumerable projections from the inner surface of the mucous membrane shaped like minute fingers; they are only found in the small intestines, and have been calculated by Colin to amount to forty or fifty millions in the horse and ox. In the interior and central part of the villus is a vessel termed the *lacteal;* it may be single or multiple, straight or branched, and at the base of the villus it opens by a valvular arrangement into the lymphatic system. Surrounding the lacteal is a network of capillary bloodvessels, while filling up the finger of the villus, not otherwise occupied by vessels, is a peculiar structure found especially in lymphatic glands, and known as adenoid tissue (p. 266) ; this tissue is relatively larger in amount in the villi of carnivora than of herbivora (Fig. 85). Covering the adenoid tisue is a basement membrane on which is set a layer of columnar cells, placed so that their narrowest end is next the basement membrane, and their broadest at the surface of the villus. The cells at their narrowest part are in touch with the adenoid tissue of the villus. Each cell contains a nucleus, and on that edge next the interior of the bowel is a clear band bearing fine striations. Lying between the columnar cells are others which from their shape are spoken of as 'goblet cells' (Fig. 86) ; by means of a pore they extrude their contents, consisting of a transparent material known as mucin, into the intestine. Within the villus are bands of involuntary muscle fibre arranged parallel to the axis of the villus, by the contraction of which, combined with the peristaltic movements of the intestine, the capacity of the lacteal vessel is altered in such a way that it is alternately filled with lymph from the reticular adenoid tissue, and emptied of lymph into the lymphatic vessel at the base of the villus. This is known as the pumping action of the villus, and provides an important factor in the furtherance of the chyle (lymph) towards the thoracic duct.



DOG. RABBIT.

FIG. 86.—TRANSVERSE SECTION OF VILLI OF CARNIVOROUS AND HERBIVOROUS ANIMALS (WALLER, AFTER HEIDENHAIN).

The large cells in the epithelial zone of the dog are the goblet cells.

The other lymph radicles found in the intestine are the *Solitary Follicles*, which are found studding the whole of the mucous membrane of the small intestines ; these solitary follicles are, at certain places in the ileum, collected into masses, where they are known as *Peyer's Patches*.

The **Solitary Follicle** is essentially a lymphatic structure, and is not concerned like the villus in absorbing anything from the food. It consists of a mass of adenoid tissue, the network of which is filled with leucocytes ; within the network are capillary bloodvessels, and surrounding the whole is a space across which branches of the adenoid network pass. This space is known as a *lymph space or sinus ;* it is lined, like those previously described, with epithelioid plates, and opens into a lymphatic vessel. As the lymph passes through the adenoid tissue, some of the corpuscles found in the meshes of the network are added to it, and become lymph corpuscles.

Chyle is a turbid fluid of alkaline reaction and a specific gravity of 1007 to 1022. In starving animals it is transparent owing to the absence of fat, and it is, in fact, at this time practically pure lymph. Colin observed that the chyle of herbivora was yellowish or yellowish-green ; it is possible that this colour may be due to chlorophyll taken up from the food. In the horse, as collected from the thoracic duct, it is often blood-stained, due, as we have seen, to leakage from the vena cava.

In the small intestines of the horse it has been observed by Colin that almost immediately after food has been given waves of chyme are passed into the duodenum from the stomach ; in consequence, the lacteals in the mesentery in connection with this portion of intestine become opaque, though previously they were filled with a colourless fluid. As the chyme passes along the bowel the other lacteals in their turn become opaque, until at last the whole of them are filled with this milky fluid. Colin draws especial attention to this regular invasion of the lacteals from the duodenum to the ileum.

The movement of chyle is due to the rhythmical muscular contractions of the walls of the intestine, and to the muscular contraction of the intestinal villi forcing it onwards, while the valves in the lacteals prevent its return. Its subsequent passage into the general circulation has already been traced.

SECTION 3.

Absorption in General.

The activity of absorption, especially in the horse, has been made known to us by the experiments of Colin.

Absorption from the Respiratory Passages is remarkably rapid. Colin showed that potassium ferrocyanide could be detected in the blood two minutes after being injected into the trachea, and that it appeared in the blood before it was found in the chyle; the same salt was also found in the urine eight minutes after being introduced into the trachea. A solution of nux vomica injected into the trachea produced tetanic symptoms in three minutes; turpentine, alcohol, and ether were also rapidly absorbed, but oil could not be taken up, and was rejected by the nostrils.

Such drugs as morphia, pilocarpine, physostigmine, etc., are all rapidly absorbed from the air passages,* and produce their physiological effect in a shorter time than when simply injected under the skin. The lungs also have the power of absorbing certain poisons such as curare, which are not absorbed when introduced into the digestive canal. The absorption of water from the bronchial passages is very rapid. Colin introduced 6·8 litres (6 quarts) of water per hour into the trachea of a horse; the animal was destroyed at the end of three and a half hours, and no fluid was found in the bronchi. He also poured into the air passages 568 c.c. (1 pint) of water at a time; repeating this without intermission, he poured in 42 litres (74 pints) of water before he caused death. So rapid is absorption from the bronchi, that a horse may be placed under chloroform almost instantaneously by an intratracheal injection of the drug.† The rapidity of absorption is therefore very great, but in spite of the facility with which drugs are taken up, the lining membrane of the bronchial tubes is remarkably tolerant of such irritating agents as turpentine, strong liquid ammonia, acetic acid, etc., and offers in a state of health an almost impassable barrier to putrid organic infusions, or at any rate these do not appear to produce any local irritation when injected.

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* It is interesting to observe that the injection of liquids into the trachea (either high up, or as low as its bifurcation) excites the reflex act of swallowing, probably due to stimulation of the sensory fibres of the inferior laryngeal nerve.

† It is not intended here to recommend the intratracheal administration of chloroform, which is not only dangerous, but produces the greatest excitement in the patient.

Absorption from the Cellular Tissue is very active, and both the bloodvessels and lymphatics take part in the process; ferrocyanide of potassium injected into the face has been detected in a carotid lymphatic in seven minutes. The rapidity of cellular tissue absorption is hastened by muscular movement.

Absorption from the Conjunctiva is very pronounced for some drugs, such as atropine and certain organic poisons, but there are others which are not absorbed so readily. Curare is not absorbed through the conjunctiva, and Colin could not infect horses with anthrax by placing anthrax blood and fluids in the conjunctival sac.

Absorption by the Skin, if the surface be unbroken, is as a rule slow even for those drugs which will pass through it, while there are many organic and inorganic substances which refuse to pass through the unbroken epidermis. Colin kept the lumbar region of a horse wet for five hours with a solution of ferrocyanide of potassium; the salt was detected in the urine in four and a half hours, although the skin was quite unbroken. In the dog absorption from the skin of such drugs as carbolic acid is rapid and frequently fatal, even in a very diluted form. From a wound or abraded surface, absorption will occur rapidly with some agents, slowly with others. Colin placed a horse's foot with a wound on the coronet in a solution of ferrocyanide of potassium; in twenty minutes he detected the salt in a lymphatic of the thigh. In connection with absorption from a wounded surface, he found that the poison was taken up quite as readily by the lymphatics as by the bloodvessels. The mucous membrane of the vagina was found by experiment to absorb very slowly.

Experiments made on **Absorption from the Pleural and Peritoneal Cavities** showed that such drugs as strychnine rapidly produce fatal symptoms when injected into these sacs; even in such a short time as from three to seven minutes tetanic symptoms supervene. Potassium iodide injected into the peritoneal cavity of a sheep may be detected in the thoracic duct five to eight minutes after the operation. Starling and Tubby have shown, however, that the active agents in absorption from these sacs are the bloodvessels, and that the share taken by the lymphatics is insignificant; for if methylene blue be injected into the pleural cavity the dye appears in the urine long before any trace of colour can be perceived in the lymph flowing from the thoracic duct.

Stomach Absorption, or, rather, its absence in herbivora, has been dealt with at p. 201. Even in the dog it is now admitted that absorption is by no means so certain as was at one time supposed. Water, for instance, passes through the stomach and undergoes no absorption; salts are only absorbed with difficulty; sugars and peptones are taken up, but only if in sufficient concentration; ordinarily they are absorbed with difficulty.

Intestinal Absorption.—The absence of stomach absorption in the horse and ox points to intestinal absorption as being of considerable importance in herbivora. That this absorption is very rapid is proved by Colin's experiments. Hydrocyanic acid injected into the small intestine of a horse caused death in one to one and a half minutes, and potassium ferrocyanide injected into the bowel, after tying the mesenteric lymphatics, was detected in the blood six minutes afterwards.

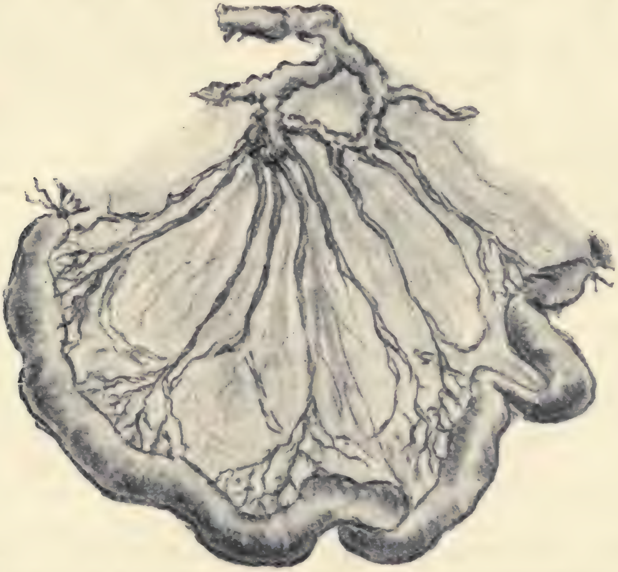

FIG. 87.—LOOP OF SMALL INTESTINE OF THE HORSE DURING ACTIVE ABSORPTION, WITH DISTENDED LACTEALS.

The Paths of Absorption.—The paths by which intestinal absorption occurs are (1) through the villi into the lacteals, and (2) through the bloodvessels into the venous system. This points to the fact that some substances taken up from the bowel may at once pass into the blood via the thoracic duct (Fig. 87), while others must first proceed to the liver by the portal vessels for further elaboration before entering the blood.

It will be remembered that the villi are found only in the small intestines; in the large intestines there are no villi. It must not, however, be supposed that absorption in the latter is exclusively carried on by the bloodvessels, for remembering the large chain of glands, along the colon in particular, it is probable that the material absorbed passes through these glands to a greater or less extent, as in the mesentery, before entering the circulation. There is, at any rate, a well-developed lymphatic system in the walls of the large intestine, and it is certain that material is taken up from this bowel both by the bloodvessels and lymphatics. The amount of this must be considerable, when the size of these bowels is borne in mind and the character of their contents.

Substances can be taken up with extreme rapidity from the large bowels. Colin observed that eighteen minutes after injecting a solution of nux vomica into the cæcum of the horse convulsions began, and eight minutes later the animal was dead. Anæsthetics, such as ether, may also be administered per rectum and produce narcosis. Finally, and from some points of view most important of all, proteids may be absorbed from the rectum and single colon, in spite of the fact that there is no proteolytic ferment to render them soluble.

Absorption of Fat.—If a cannula be placed in the thoracic duct of a starving dog, the lymph which escapes is identical with that from any other part of the body. If the animal be now fed on a diet rich in fat, the lymph becomes milky, and even the blood plasma becomes turbid from fat, if the contents of the duct are permitted to enter the general circulation. It is evident that the lymphatics are the chief path by which the fat enters the body, for comparative analysis of the blood of the portal vein and carotid artery shows that the amount of fat in the two is the same. Nevertheless, the bloodvessels are not without some action in the matter, the evidence being that from an open thoracic duct not more than 60 per cent. of the total fat given in an experimental diet can be recovered; after deducting that excreted unabsorbed with the fæces, there still remains a balance unaccounted for. The missing portion of fat is believed to be absorbed by the bloodvessels.

It has been shown (p. 256) that fat in the small intestine is both saponified and emulsified, the former being a chemical, the latter a physical change. These processes result from the separate and combined action of the pancreatic juice and bile, and they lead to two possible views as to the mechanism of fat absorption. Emulsification reduces the fat (and fatty acids) to a state of subdivision into particles so minute that they might conceivably be simply passed as such, through the epithelial cells of the villi to the lacteals, by an activity of these cells comparable to the ingestive powers of a white blood-corpuscle. This would readily account for the appearance characteristic of chyle (p. 278), the minuteness of the fat particles it contains being probably intended to prevent embolism by plugging of the capillaries. The view thus indicated was the one formerly most prevalent. On the other hand, bile has, in virtue of its bile-salts, an extremely active solvent action on both fatty acids and soaps: hence the possibility that fat is split up so as to give rise to variable relative amounts of substances, which pass *in solution* into the cells of the villi, as do the proteids and carbohydrates. We shall see that the chemical view is the one now generally adopted.

If the intestinal mucous membrane of an animal in full fat absorption is stained with osmic acid, the epithelial cells are found to be crowded with minute particles of varying size, whose blackness shows them to be fat (Fig. 88). This fact provided the chief support for the view that fat reaches the lacteals in a state of minute mechanical subdivision not necessarily involving much chemical change. If this were so we should expect to see some of the fat particles in transit through the striated border of the epithelial cells, and this is never observed.

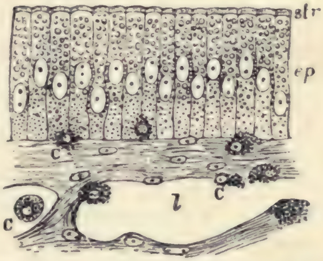

FIG. 88.—MUCOUS MEMBRANE OF FROG'S INTESTINE DURING ABSORPTION OF FAT (SCHÄFER).

ep, Epithelial cells; *str*, striated border; *c*, lymph corpuscles; *l*, lacteal.

It is generally accepted that the fat passes into the cell and not between the cells, and the question arises as to whether this passage into the wall of the bowel is a physical or a secretive process. Leucocytes are not credited with absorption, though as carriers of fat between the epithelial cells and the central lacteal—viz., through the arterial network of the villus—they undoubtedly assist. On the other hand, the absorption of anthrax bacilli from the intestine, a process which is undoubted, must occur by their being engulfed by cells. The wandering cells of the body are, we know, capable of ingesting bacteria in other places, and there appears no reason why it should be different in the intestines. Nevertheless, there are good reasons for believing that the fat is dissolved and absorbed by the epithelium of the intestine, its solution into fatty acids and glycerin being effected by the combined action of the bile-salts and pancreatic lipase. These split products are readily absorbed, glycerin presenting no difficulties, while the fatty acids are taken up either as such or as soaps. It has been stated that osmic acid staining reveals the fact that fat as such exists in the epithelial cells. It is evident from this that the fats after solution are reconstructed into neutral fats within the epithelial cells. The synthesis of fats in the intestinal epithelium is effected by the same ferment, lipase, which originally split it up; it is not difficult to imagine a reverse action of lipase in order to bring this about. If an animal be fed on fatty acids without glycerin, neutral fats are found in the thoracic duct. Somewhere, therefore, the fatty acids have picked up glycerin, and this is believed to be in the intestinal wall, lipase effecting the reconstruction. The story is interesting and instructive; it emphasises the specific and selective influence of the living cell, regarding which further evidence will be given later. In the above process the valuable action of the bile-salts in dissolving the fatty acids, and so assisting the lipase of the pancreatic secretion, is very evident.

When an animal is receiving a known quantity of fat in the food, and the whole of the chyle from the thoracic duct is collected with the object of recovering it, a portion of the fat is found to be missing. In these circumstances only 60 per cent. of the fat can be recovered from the chyle, and that which is missing is believed to be absorbed by the bloodvessels of the villi as fatty acids and soaps, and taken to the liver before its entry into the general blood-stream. This receives further support from the fact that after ligature of the thoracic and right lymphatic duct, 30 to 40 per cent. of fat are absorbed from the intestine. Even after excision of the pancreas, fat absorption is not entirely abolished, and strange to say, more may be found in the intestinal canal than was given by the mouth. This suggests that fat may even be excreted by the intestinal wall.

All fats are not equally absorbed. In the dog olive oil is taken up more completely (97 per cent.) than any other; next comes mutton fat, of which 90 to 92 per cent. are absorbed; while of spermaceti only 15 per cent. are taken up. A dog may absorb up to 21 per cent. of fat in three or four hours, double that in seven hours, and 86 per cent. in eighteen hours. Absorption of fat, in ruminants especially, is a most important question, considering the large sums spent in adding this to the diet of animals intended for food. Experimental inquiry shows that 90 per cent. of the fat in linseed cake, 79 per cent. in rape cake, and 88 per cent. in decorticated cotton cake can be absorbed. The digestion of the horse for fat is lower than that of ruminants; only 53 per cent. of the fat in linseed cake can be utilised by this animal.

The following table shows the power possessed by the herbivora of absorbing fat from different food substances, and demonstrates the relatively weak powers of the horse in this respect :

	Horse.	Ruminant.
	Per Cent.	Per Cent.
Grass	20	66
Hay	24	50
Oats	70	83
Barley	42	89
Maize	61	85
Beans	13	86

All the above foods in the matter of fat, and we shall see presently in the matter of carbohydrates and protein, are richer and more nourishing for the ruminant than the equine, owing to the different powers of absorption in the two classes.

Food-Absorption.—At this point it is necessary to digress somewhat, and glance at the question of the absorption of the various proximate principles of food—viz., protein, fat, and carbohydrate.

The economic feeding of animals has led to the chemistry of food-absorption being inquired into by laborious series of experiments which have been carried on for years. Each class of animal has a different power of utilising the same food ; for example, grass and hay are far more nourishing to the ox and sheep than to the horse, and the ox can utilise more than the sheep.

If a food were entirely digested and absorbed, there would be no fæces excepting the waste liquid secretion of the digestive tract. There is, of course, no ordinary food substance capable of complete absorption ; there are indigestible substances which cannot be dealt with and are excreted ; and with the herbivora these must necessarily be very large. But entirely apart from indigestible matter, there is only a proportion of each of the proximate principles of a food which can be absorbed. The protein, fat, carbohydrate, and cellulose of every food substance has a distinct rate of absorption in each class of animal. Taking hay as an example, the horse can, as a mean, digest :

	Per Cent.
Protein	57
Fat	24
Carbohydrates	55
Cellulose	36

In no way can a given amount of hay be rendered more efficient by causing more to become absorbed. Absorption of the food principles is unaffected by rest or work. The horse absorbs no more per cent. if the diet is increased ; he can extract no more per cent. if the amount be reduced. Feeding experiments show that around 57 per cent. protein and 55 per cent. carbohydrates lies the digestive capacity of the horse for these proximate principles in hay.

If we take the figures for the ox and sheep, for the purpose of comparison, we get the following table :

	Ox.	Sheep.
	Per Cent.	Per Cent.
Protein - - - -	57	57
Fat - - - - -	49	51
Carbohydrate - - -	62	62
Cellulose - - - -	58	56

These facts are of extraordinary importance in the feeding of animals. The practical conclusions to be drawn from them belong to the realm of hygiene. They are mentioned here owing to their physiological aspect, for though we cannot explain the reason, there is no doubt that both ox and sheep in the matter of food absorption are physiologically superior to the horse, while no animal approaches the pig in the thoroughness with which absorption and consequent utilisation of food substances occurs.

Absorption of Carbohydrates.—We have seen (p. 256) digestive changes undergone by starch in order to prepare it for absorption, and we have learned that in the body only the simple sugars, such as dextrose, levulose, and galactose, but especially dextrose, are capable of being utilised, while the complex sugars—lactose, cane sugar, and maltose—have all to be reconstructed in order to fit them for absorption. The following brief summary shows by what means the carbohydrates are prepared for entry into the body :

Starches are converted by means of the saliva and the *amylase* of pancreatic juice into maltose and dextrin, and then inverted by the ferment *maltase* into dextrose.

Lactose requires inversion by *lactase* into dextrose and galactose.

Cane sugar requires inversion by *invertase* into dextrose and levulose.

If an attempt be made to cause the organism to use up such sugars as cane sugar without passing it through the inverting process, as, for example, by injecting it subcutaneously, it is excreted unchanged in the urine.

If very large amounts of cane sugar, or even dextrose, be given, they are taken up unaltered, probably by the lacteal vessels, and excreted by the kidneys. This constitutes the temporary glycosuria which sometimes follows a diet rich in carbohydrate. The lacteal path of absorption is of interest, for, as we shall see presently, physiologists have assigned the bloodvessels as the path by which sugar is taken up. Nevertheless, years ago Colin insisted that in the herbivora the chyle vessels took up sugar. The chyle of a horse on an ordinary diet of hay and oats was found by him to yield 13 to 16 per cent. sugar, and several such observations are referred to by him in terms which lead one to believe his experiments were adversely criticised by Bernard. The physiologist of the present day regards the bloodvessels of the villus as the path by which the sugar mainly gains entrance to the body. From here it is carried to the portal vein, and passes direct to the liver. We have seen (p. 246) that the sugar percentage in the portal vessel may vary: 0·4 per cent. has been found after a heavy carbohydrate meal in the dog, and 0·2 per cent. in the same animal during starvation. On the other hand, a definite percentage is maintained in the other vessels of the body, and the cause of this has been fully considered elsewhere (p. 249).

The absorption of carbohydrate by the animals of the farm has been the subject of considerable investigation. The ruminant in all cases is better in this respect than the horse, as may be seen from the following table:

	Horse.	Ox and Sheep.
	Per Cent.	Per Cent.
Hay - - - -	24	50
Clover hay - - -	29	53
Oats - - - - -	70	83
Barley - - - -	42	89
Maize - - - -	61	85
Beans - - - -	13	86

The practical application of these facts is very evident. All the above foods in a given quantity are richer for the ruminant than the horse. In dieting horses, according to the market value of grain, it is well to ascertain what proportion of its proximate principles are digested, or it may prove far from economical.

Absorption of Proteins.—Proteins, we have seen, are incapable of absorption as such. *Pepsin*, *trypsin*, and *erepsin* convert them into peptones and proteoses, and in this form, or when still further broken down by *trypsin* and *erepsin* into amino-bodies, they are taken up by the bloodvessels of the intestine.

It is not known to what extent the hydrolytic action is necessary before absorption can occur ; certainly it must be carried as far as proteoses and peptones. If the thoracic duct of a dog be ligatured, and a large protein meal given, it is perfectly absorbed as shown by the increase in urea. Clearly the path of absorption for protein is the bloodvessels, the material passing by the portal vein to the liver. From this it might be supposed that proteose and peptone may readily be found in the general circulation, but as a matter of fact, there is no blood in the body, including that of the portal area, which contains even a trace of peptone or proteose ; in fact, these substances in the circulating blood are poisons, give rise to peptonuria, and are excreted by the kidneys.

Proteose and peptone in their passage through the epithelial cells of the intestinal wall are resynthetised. How and in what way this is brought about is unknown. We saw that the same thing occurred to the fats before they could pass into the lacteals. Proteins administered by any other channel than the digestive canal are excreted — egg-albumin, for instance, if injected into the blood and got rid of by the kidneys. Foreign proteins are of no use until they have passed through the proper laboratory —viz., the intestinal canal—and that something more than splitting the complex protein molecule occurs is evident from the fact that some rearrangement of the molecule occurs which enables it now to be built into and form part of the protein tissues of the living body.

The absorption of protein by animals is an important question in feeding. We saw that, in the matter of fat and carbohydrate, the horse was distinctly inferior to ruminants in capacity for absorbing these substances. In the matter of protein absorption the horse is sometimes superior to the ruminant, and in all cases holds his own, as may be seen from the following table :

	Horse.	Ruminant.
	Per Cent.	Per Cent.
Fresh grass - - -	59	70
Hay - - - - -	57	57
Wheat straw - - -	19	17
Oats - - - - -	79	79
Barley - - - -	80	70
Maize - - - -	77	74
Beans - - - -	86	88

Absorption of Water and Salts.—By means of the bloodvessels water is readily absorbed, though all parts of the digestive tract are not equally active in this respect. There is probably no absorption of water from the stomach of any animal. There is very little absorption of this fluid from the small intestines, whereas in all animals the large intestines are the chief seats of absorption. In the horse the cæcum, in other animals the large colon is the chief seat.

In the matter of the absorption of salts, a good object-lesson of the peculiar selective powers of the epithelial cells is obtained. Chlorides are readily taken up, but sulphates only with difficulty; iron is taken up, but its near ally, manganese, is absorbed with difficulty. Though these facts suggest that the process is one of secretion rather than the result of physical action, yet it is impossible to neglect physical factors as playing a part. Finally, Colin's experiments on the herbivora showed that absorption of salts, such as prussiate of potash, iodide of potassium, tartar emetic, and many other substances and colouring matters such as chlorophyll, occurred by the chyle vessels, though not necessarily exclusively.

Much of the foregoing refers to absorption from the small intestine, but it would be wrong if we failed to emphasise the fact that in the herbivora especially the large intestine is the seat of vitally important digestive processes. An attempt has been made (p. 220) to deal with these in the light of our limited knowledge, but it is a very imperfect picture. It is only referred to here in order to emphasise the fact that the large intestines, though they present no villi and no secretion other than the succus entericus, are important seats of digestion and absorption. A man may manage to get along without his large intestines, the horse could manage if he had half the present length of small intestine, but he could not afford to spare an inch from his large bowels. From imperfect knowledge, and the difficulties attached to experimental inquiry in the larger animals, we do not know the absorptive function of any portion of the large intestine excepting the bare fact that it does absorb. At p. 219 attention is drawn to the remarkable fact that a few inches in the intestines of the horse separate fluid fæces from solid fæces. Who can doubt the important changes which must be taking place in those few inches? The ox and sheep are in their anatomical arrangement very similar—almost identical, in fact. Their diet is identical, perhaps their digestive processes identical, up to a certain point; then they differ widely: the fæces of the sheep are firm and dry, those of the ox soft and unformed. There must be important differences in the intestinal absorption of animals so nearly related.

CHAPTER VIII

DUCTLESS GLANDS AND INTERNAL SECRETIONS

THE **ductless glands** of the body are represented by the spleen, thyroid, thymus, adrenals, pituitary, and pineal bodies. The function of these is either imperfectly known or entirely unknown, but within recent years experimental inquiry has thrown some light on their use as glands producing an *internal secretion*—viz., a something carried away by the blood or lymph stream, and utilised elsewhere by the body.

Internal secretions are not limited to ductless glands. It is now known that the pancreas, liver, and other glands produce, in addition to the visible secretion passing away by their duct, another or internal secretion, which leaves by lymph or blood channels, and is quite distinct from the ordinary fluid secreted by the gland (see also p. 261).

The discovery of *secretin* (p. 252) by Starling and Bayliss opened up a field of the highest importance, possessing possibilities the extent of which cannot be forecast. In *secretin* we have a specific chemical excitant, or *hormone*, and it may yet be shown that secretions which have been regarded as due to the influence of the nervous system are in reality produced by a chemical stimulant furnished by the body itself. Edkins, indeed, considers this is so of the gastric juice, while Starling and Bayliss point to the specific chemical excitant theory as offering some explanation of the sympathy between the uterus and the mammary gland, the occurrence of menstruation, also of periodic sexual excitement in the lower animals. The ovary has been suggested as the seat of production of such chemical excitant. The corpus luteum is regarded as a ductless gland, its internal secretion being connected with the fertilisation and implantation of the ovum. The influence of the ovaries on the development of the external genital organs may also in this way be explained, for the arrested development which occurs as the result of removing the ovaries in the young animal is prevented by implanting them in a distant part of the body.

The sympathy between ovaries and mammary glands is further shown by the remarkable fact that a cow ovariotomised when in *full milk* remains in milk for two or three years. The influence of the ovaries on psychic conditions is well recognised: some forms of vice in the mare are cured or improved by removal of the ovaries. It is to be noted that apparently the complete removal of all trace of ovarian tissue in the cat and dog may not invariably prevent periodic sexual excitement (Leeney). It has been stated that the removal of the ovaries from the dog affects metabolism, especially the consumption of oxygen, which falls off, and that this may be neutralised by the administration of an extract of ovary; this causes the metabolism to rise above the normal, but does not affect the unoperated animal.

Similarly, there can be no doubt as to the testicles forming an internal secretion. It is fair to assume that among other functions the implantation of the characteristics of the male, especially the aggressive characteristics, must be regarded as part of its duty. Otherwise it is difficult to account for the alteration in character which occurs as the result of complete castration, and the modifying change which follows from leaving some of the epididymis attached to the cord. Castration does not appear to lead to any important loss of muscular energy or power of withstanding fatigue. The influence of the testicles on the growth of bone is recognised in man; the long bones continue to grow, due to the delay in the ossification of the epiphyses; the same is said to have been observed in animals, but of this, so far as we know, there is no evidence. The effect of castration on the eating properties of flesh is well known. Its influence on the thymus gland is also very marked; instead of disappearing at puberty, castration causes the gland to become larger and more persistent. The effect of removal of the testicles and ovaries on the dog, cat, deer, and birds, may be conveniently considered in the chapter on Generation and Development.

The adaptation of the digestive fluids to the nature of the food has been referred to (p. 192). This and the influence of a fixed diet in producing a more effective digestive secretion, and the harm resulting from sudden changes in diet (p. 257), may possibly be regulated by a specific chemical excitant. These are matters of the highest practical importance in the feeding and management of animals.

The chief lesson that the present work on internal secretions teaches is that an organ apparently functionless may be performing some office of the highest importance, while even those actively employed in the preparation of an obvious secretion may, in addition, be carrying out important chemical activities —the liver, for example, with its external secretion of bile and its internal secretion of urea and glycogen ; the pancreas, with its digestive fluid, and its invaluable internal secretion, which regulates the destruction of sugar. Even the kidney, in all probability, possesses an internal secretion affecting metabolism. The spleen, on the other hand, would appear to possess neither an internal nor an external secretion, for it has frequently been removed without ill effects ; but the question must be dealt with in a little more detail.

The **Spleen,** in spite of the numerous observations to which it has been subjected, is still a physiological enigma. Its vascular arrangement is peculiar in that it is capable of holding a considerable quantity of blood, and for this purpose readily lends itself to change of size. Further, it is the only tissue in the body where the cell elements are directly bathed in blood without the intervention of even a capillary wall. The spleen contains a considerable amount of involuntary muscular fibre and is capable of movement. These movements have been carefully studied, and it is established that they are of two kinds. One is a slow expansion due to unknown causes, which occurs after a meal ; it reaches its maximum about the fifth hour, and is followed by contraction. The other is a rhythmical expansion and contraction occurring in certain animals, such as dogs and cats, at intervals of about one minute. It is believed that the latter movement is for the purpose of assisting the circulation through the organ, to which the splenic pulp offers considerable resistance. That the movement is brought about by the bands of involuntary muscular fibre is undoubted ; the spleen is liberally supplied with motor nerves carried in the splanchnic, and stimulation of these leads to a reduction in the volume of the organ. It is also considered that there are nerves to the spleen, which on stimulation produce dilatation.

The *use of the gland* is largely based on conjecture. By some it has been considered the seat of formation of red blood-corpuscles, and that this is the case during intra-uterine life and shortly after birth is undoubted ; but there is no evidence of this function in the adult. It has been claimed to be the seat of destruction of the red cells and of phagocytosis, and on this point there are some telling facts ; for instance, certain large amœboid cells found in the spleen are capable of ingesting and destroying worn-out blood-cells and other solid matter such as micro-organisms, while the richness of the splenic pulp in iron is regarded as due either to the hæmoglobin of the destroyed red blood-cells being stored up for future use, or to the preparation of new hæmoglobin. That the conservation of iron is one of the functions of the spleen, would appear from the fact that removal of this organ in dogs causes a distinct daily loss of iron.

The theory is very plausible, though by no means definitely proved; at the same time there is great difficulty in getting away from the fact that the spleen appears in every way to be admirably suited to act the part of a blood filter.

The lymphoid tissue of the spleen, like that of lymphoid tissues in general, is capable of forming a substance from which uric acid may be readily produced, and the spleen has in consequence been regarded by many as the seat of active metabolic changes with the formation of uric acid. The evidence, however, is not sufficiently conclusive to warrant uric acid being regarded as a special product of the spleen.

Some physiologists have suggested that the spleen produces an enzyme which converts trypsinogen into trypsin. There is no reason why the spleen might not do so, but it by no means follows that this is normally its function, nor would there appear to be any necessity for this action in face of the fact that it is one of the special duties of the intestinal juice.

In connection with all these theories it is well to remember that the spleen may be removed completely, and no ill effects follow.

Thyroid and Parathyroid Glands.—Some of the most interesting work on the ductless glands has been carried out on the thyroid, and it is largely to this body that such little knowledge as we as yet possess of internal secretion is mainly due.

For years it had been observed that atrophy or absence of this gland in the human subject was associated with arrested development both mental and physical; the man so affected remained a child both in intelligence and appearance. This stimulated experimental inquiry, and the thyroids were removed in many animals, the majority of carnivora dying as the result, while half of the herbivora recovered from the operation. So contradictory were the results obtained by different observers on the gland and its uses, that the whole question was submitted to very close inquiry, which revealed the fact that the ordinary thyroid consists of two distinct portions, one part the *thyroid* proper, the other the *parathyroids*. Considerable variation exists as to the arrangement of the thyroids and parathyroids. As a rule there are four parathyroids—an anterior and posterior pair. The latter, in the herbivora, are closely embedded in the capsule of the thyroid, but there are great variations in arrangement even in the same species. In most animals much the same results are obtained when both parts are removed, but when the parathyroids alone are excised, death rapidly ensues, preceded by convulsions. The removal of the thyroid only gives rise to a train of symptoms accompanied by chronic wasting and malnutrition, much slower in development than in the case of the parathyroids. The convulsions attending removal of the parathyroids are said to be abolished by injections of extracts of the gland. Recently it has been shown that injection of calcium salts effects a cure of all the symptoms produced by removal of these bodies. The colloid substance constitutes the internal secretion of the thyroid, but forms no part of the secretion of the parathyroids ; and histologically while the former consists of vesicles lined by a single layer of cubical epithelium, the parathyroid is composed of columns of epithelium-like cells. The gland contains a nucleo-protein and colloid substance ; the latter is not a nucleo-protein, and is remarkable for containing iodine in organic combination with the proteid. The iodine-containing substance is termed *iodothyrin* ; it is a brown amorphous material, containing phosphorus and 10 per cent. of iodine. The parathyroids contain no iodine.

As to the use of these bodies, it is now generally accepted that the internal secretions of the parathyroids and thyroids are not the same. It is believed that the parathyroids are intended to neutralise some poisonous substance produced in the body during metabolism ; hence, with their removal, the toxic substances accumulate in the blood. It would also appear that in some way or other they may be connected with calcium metabolism. The functions of the thyroid are equally obscure ; they appear to be connected with the metabolism of the central nervous system. The colloid iodine-containing substance is probably the active principle, as therapeutically it takes the place of thyroid tissue. Whether this is due to its containing iodine is not decided, but extracts of the gland which are rich in iodine give better results in treatment than glands poor in that substance.

Thymus.—This body, composed of modified lymphoid tissue, is mainly of use in fœtal and very early life ; later on it atrophies. Nothing is known of its function, though it is observed that castration appears to have an effect on its disappearance. The process of atrophy is much slower in the castrated as compared with the uncastrated animal, while its early absorption has been observed to be associated with a rapid growth of the testicles.

Adrenals.—The experimental removal of the adrenals in any animal is rapidly followed by death, preceded by symptoms of great muscular prostration and diminution of vascular tone. In Addison's disease in man these bodies are affected, and give rise to much the same symptoms as above, and in addition bronzing of the skin is present. Like the thyroids, the adrenals consist of two distinct tissues, a medulla, which can be shown to be derived during the process of development from the sympathetic nervous system, while the cortex is formed from the mesoblast. While nothing is known of the function of the cortex, the medulla yields under experimental inquiry some remarkable and characteristic results.

An extract of the medulla of the gland when injected into the blood increases both the rate of rhythm and tone of the cardiac muscle, and causes a contraction of the bloodvessels, which produces a remarkable increase in blood-pressure. This increase is of a purely temporary nature, which indicates that the active principle is destroyed in the circulation. Within a few minutes the heart-beats return to the normal and the blood-pressure falls. The active principle known as *adrenalin* can be detected in the veins leaving the gland, so that there can be no doubt that it is poured into the blood, where it regulates the rhythm and tone of the heart-muscle and maintains blood-pressure. In this important function the adrenals are probably assisted by another internal secretion, to be looked at presently —viz., that from the pituitary body.

The action of adrenalin in causing constriction of the blood-vessels is turned to account in minor surgery in controlling hæmorrhage.

It is believed that the adrenals possess secretory nerve-fibres derived from the splanchnic, and stimulation of these increases the amount poured into the vein of the gland. Adrenalin acts upon all plain muscle and gland-cells which receive sympathetic fibres, and it is distinctly noteworthy that the effects are identical with those produced by stimulation of the sympathetic fibres (Langley), of which system the medulla of the gland is, as pointed out above, merely an outgrowth.

It is probable that the function of the medulla of this gland is concerned in the provision of a substance intimately connected with muscular metabolism, especially 'tone,' not only of the skeletal muscles, but also of the muscular fibres of the circulatory system. There is also considered to be some connection between the cortex of the adrenals and the sexual system. In rabbits the cortex of the gland becomes twice the normal thickness during pregnancy; and it is believed that in man a connection exists between the adrenals, the growth of the body, development of puberty, and sexual maturity.

The Pituitary Body.—This gland consists of an anterior and posterior lobe, the former being glandular in nature, the latter nervous in structure. It is believed that the anterior lobe is connected in some way or other with the nutrition of the skeleton. Enlargements of the pituitary are associated with a singular disease in the human subject—*acromegaly*—characterised by an overgrowth of the bones of the face and extremities. The posterior lobe resembles the adrenal medulla in its action on the heart, bloodvessels and skeletal muscles generally, but with certain marked differences. An extract of the posterior lobe increases the tone of the heart-muscle, but not its rate of rhythm, and though it constricts the arterioles generally, it causes dilatation of the kidney. Schäfer, whose work we have followed, also points out that the pituitary contains a substance which diminishes the force of the heart-beat, and inhibits the contraction of the arterioles, and that this, though overbalanced in the artificial extract by the opposite effects, may, under physiological conditions, be poured into the blood in such quantities as the muscular system needs. One other possible function of the pituitary may be referred to, and that is the influence of extracts in producing a tonic effect on the nervous system, and so assisting in maintaining not only the proper balance of the circulation, but of tone, in the nerve centres generally.

Nothing is known of the uses of the **Pineal Body,** an organ regarded as the dorsal eye of a remote ancestor.

CHAPTER IX

THE SKIN

It is obvious that one important function the skin performs is that of affording cover to the delicate parts beneath; whereever the chance of injury is the greatest, the skin is the thickest, while in those parts where sensibility is most required it is thinnest. The skin of the back, quarters, and limbs are good examples of the first type; on the back especially, a protective covering is found which, in some horses, is as much as ¼ inch in thickness: the face and muzzle are a good example of the latter variety, the skin in some parts being as thin as paper. In those regions not exposed to violence it is also thin, as on the inside of the arms and thighs. In spite of the thinness of the skin its strength is remarkable; a horse's body may be dragged along by the thin skin of the head.

The skin as an organ of touch is of great importance. All animals appear most sensitive to even slight skin irritation; flies will cause horses considerable suffering, and the elephant, with its thick hide, is quite as intolerant of these tormentors as is a well-bred horse. The skin is highly endowed with sensory nerves, especially that part connected with the organs of prehension; the long hairs, 'feelers,' growing from the muzzle of the horse end in special tactile structures in the skin (Fig. 89).

The skin is a bad conductor of heat, and this is considerably assisted by the layers of fat found beneath or at no great distance from it, as in the abdominal region; it is the subperitoneal fat which protects the viscera of animals living in the open and lying in wet places. The epidermal covering of the skin relieves the parts beneath from excessive sensitiveness; through the sebaceous secretion it assists in preventing loss of heat, while the greasy covering helps the hair to throw off rain, prevents the penetration of water, and so saves the epidermis from disintegration. Horn is skin which has undergone a modification.

Hair.—Not all parts of the body are covered by hair. There is very little on the muzzle and lips, and it is very scanty on the inside of the thighs, inside the cartilage of the ears, and on the mammary gland and genitals. By means of the hair the heat of the body is maintained and prevented from passing off too rapidly. The thickness of the hairy covering varies considerably with the class of horse; the better bred the animal the finer the coat. Draught horses yield between $3\frac{1}{4}$ to $3\frac{1}{2}$ kilogrammes (7 or 8 pounds) of mixed hair, dirt, and dandruff by clipping; in a well-bred horse this would be reduced to 283 grammes (10 ounces), or even less; the amount of hair of the mane and tail is about $\frac{3}{4}$ kilogrammes ($1\frac{1}{2}$ pounds). It is a well-known fact that, excepting the hair of the mane and tail, that of every other part of the body has only a temporary existence, and is changed twice a year, once for a thick, and once for a fine coat. During this period horses are generally regarded as not being at their best, and changing the coat is always urged as a cause of loss of condition or stamina. The permanent hair is not entirely represented by that of the mane and tail; the eyelashes and fetlock hair are permanent, also the long tactile hairs on the muzzle. The temporary hairs on the horse are of two kinds, which can only be distinguished by their rate of growth. If a part be clipped, or, preferably, shaved and the growth watched, in a short time it will receive a scanty covering of long, rapidly growing hair, followed by a slow growth of ordinary hair. There is no difference in the two hairs, excepting the length. The long rapidly growing hairs are known as 'cat hairs'; they are not numerous, being about 4 per square centimetre (27 to the square inch), while the ordinary hairs are nearly 700 per square centimetre (4,300 to the square inch).* It may yet be shown that 'cat hairs' are tactile in function. The growth of the hair is regulated by the surrounding temperature. If horses in the depth of winter are placed in a heated atmosphere, such as a horse deck on board ship, the majority commence to shed their winter coat in a few days,

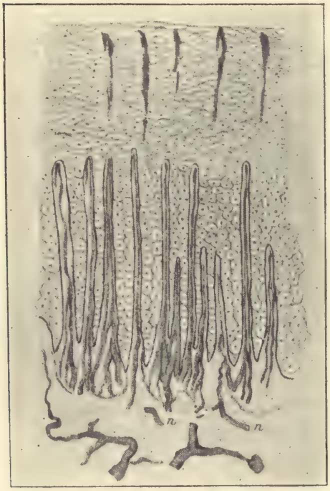

FIG. 89.—SECTION OF MUCOUS MEMBRANE OF THE HORSE'S LIP, SHOWING THE NERVE ENDINGS IN THE TOUCH PAPILLÆ.

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* I am indebted to Major Newsom, Army Veterinary Corps, for the trouble he has taken in making this tedious calculation.

though the temperature of the outside air may be at freezing-point; similarly, if taken from a warm to a cold locality, the hair responds by becoming longer. Speaking generally, the above statements are correct, but there are exceptions and modifications. Some horses do not shed their coat after passing into a warmer latitude; the mechanism which regulates the periodical shedding of hair refuses to respond to the changed condition of affairs, so that in passing from north to south of the Equator, with its reversal of seasons, the animal may grow a summer coat in winter and *vice versa* for at least a year after entering the new latitude. The permanent hair of the body — viz., the mane and tail — may grow to almost any length, but the temporary hair of the surface of the body only grows to a definite length. The full length having been attained, nothing will make it grow longer, yet if the horse be clipped, hair at once grows rapidly, but only to its original length; in other words, everything is present for the needful growth to occur, but there is a restraining influence which determines the length of hair according to the season.

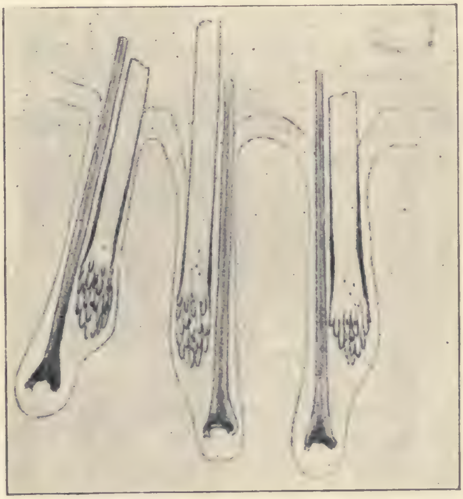

FIG. 90.—SECTION OF HORSE'S SKIN, SHOWING THE CASTING OFF OF THE OLD HAIR AND GROWTH OF THE NEW.

It will be observed that both are emerging from the same follicle.

Hair Streams.—This term has been very aptly applied to the direction taken by the hair. Very little observation shows that though the general trend of the stream is obliquely downwards and backwards on the neck and trunk, downwards on the face and limbs, and backwards on the cheeks, that, nevertheless, the stream alters its course in an interesting manner at various parts of the large surface, while vortices are frequent. The number and position of the latter are variable; indeed, it has been considered that no two horses are identically marked in this respect, and in Japan it is employed for the identification of horses on much the same lines as the thumb-print system among men. There are certain vortices seldom absent; one, the largest, may generally be seen in the flank, the hair over the loins distinctly divides as it approaches the crest of the ilium, one current passing over the quarters, another down the flank. This is met by a stream passing up the flank, which divides the hair right and left; on the left (if the near side be inspected) it passes forward and downwards over the flank, on the right it curves outwards to pass down the quarters. Another vortex may often be seen issuing from under the belly, just in front of the flank, and radiating upwards. The neck, just below the angle of the jaw, has also a vortex, and there is one on the face; but there are many others not so regular though frequently seen—for instance, on the poll, on either side of the neck, middle line of the neck, over the pectoral muscles, stifles and diffuse areas below the knees and hocks. In Fig. 91 the general direction of the body hair has been indicated. 'Feather' was the very apt term applied a century ago to the hair pattern of which we are speaking. In the present day feather is employed to designate the hair on the legs of cart horses, so that the term vortex, employed by the Germans, is adopted. It must, however, be remembered that though vortex suggests a circular pattern, many are elongated and distinctly 'feather like.'

Of the **pigment in hair** which gives colour to the coat, our knowledge, until quite recently, has been of the scantiest kind. The active investigation now being carried out of Mendel's theories of heredity, when applied to the special case of heredity in coat-colour, made it essential to know more about the origin, nature, and behaviour of the hair pigments, and so we now have some information which is both interesting and promising.* Using the name in its generic sense, three different forms of 'melanin' are found in hairs—black, chocolate, and yellow. Of these the black is extremely insoluble, and hence very difficult to deal with; as also is the chocolate pigment, though to a less extent. The yellow, on the other hand, dissolves readily in numerous solvents, and may thus be easily obtained. In its reactions it differs entirely from the black and chocolate pigments. In the case of mice there is now no doubt that their varying colours are due to the presence in their hairs of one or more of these three pigments. The less numerous experiments so far made with horse-hairs, suggest no doubt as to the different colours of horses being due to causes essentially the same as those which give the various colours to mice. As to the origin of these pigments, it has generally been presumed that they must be derivatives of hæmoglobin, but there are no pathological or purely chemical facts in definite support of this view. On the other hand, it has been shown* that an extract can be made from the skins of rats, rabbits, and guinea-pigs, which acts on tyrosine in such a way as to give rise to pigment substances.

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* Florence M. Durham (Proc. Roy. Soc., vol. lxxiv., p. 310, 1904).

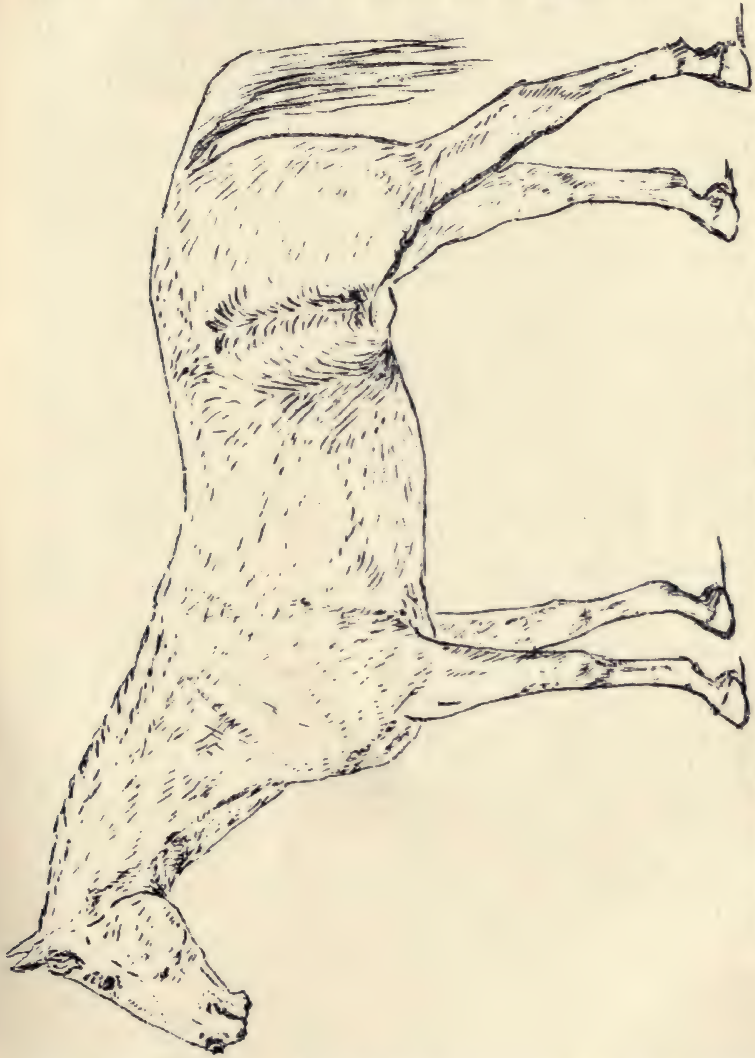

Fig. 91.—Hair Streams and Vortices in the Horse (after Ellenberger-Baum).
The lines indicate the general direction taken by the hair at different parts of the body surface.

From the conditions under which the conversion is most readily effected, and the fact that the activity of the extract is at once destroyed by boiling, the active agent is regarded as a ferment, and, in accordance with the systematic nomenclature now used, is therefore known as *tyrosinase*. A further fact of extreme interest is that the colour of the pigment formed from tyrosine corresponds to the colour of the animal from whose skin the active extract is made. Black pigments are produced when animals are used whose skin contains black pigment, and yellow substances are obtained when the skin contains orange pigment.

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* *Loc. cit.*

Colours of Horses.—The body colour of animals is protective; whatever the tint may have been in the ancestors of horses, it is intended to help in the struggle for existence. It is probable that the colour was a dun; far more protective colouring, however, is afforded another species of equine in the form of bars. The zebra under certain conditions of light is invisible. With the exception of black and grey horses, which are liable to turn grey or white, all other colours are practically permanent even to old age. We do know, however, that injuries to the skin of horses, even of a slight character, are commonly followed by a growth of perfectly white hair, which never regains its pigment. In these cases the skin also loses its pigment; pigment granules are not reproduced in injured skin. The connection between body colour and constitution is a physiological question to which, unfortunately, no answer can be given. Colour and temperament may go hand in hand; other connections are not less difficult to explain. Chestnut horses are frequently excitable, nervous, and irritable; all horses of light colour, no matter what it may be, are, as a rule, wanting in stamina and constitution. The 'mealy' bay is typical of a bad colour and almost invariably of a bad horse. Grey horses are not popular, they give too much trouble to keep clean, and show every stain, yet in the East such coloured horses are capable of great fatigue, and possess remarkable stamina, provided that the skin is pigmented. A grey horse with a pink skin is an albino, and is worthless for hard work. For work and hard constitution a roan is difficult to beat, especially a red roan, yet the colour is not popular. The 'softest' horse is the black, and on this point there appears to be no difference of opinion.

It is seldom that the colour of a horse is not broken by the introduction of white; this is common on the face and limbs, and in days gone by a star on the forehead was so prized that one was created if it happened to be absent. On the limbs the amount of white is variable; no exception is taken to it if limited, but four white legs are not only unsightly but a source of weakness. White legs are liable to 'chap' in winter, for white on the limbs of a coloured horse is associated with a pink skin; such a skin is readily affected if washed and left wet.

Grey legs, as apart from white, are usually only found in grey horses. Grey horses may have grey legs or white legs. In horses of any colour white coronets mean colourless feet, grey coronets black feet, for the reason that the skin of *grey* horses is pigmented. Black coronets yield a dark slate-coloured horn commonly referred to as black. A coronet with black-and-white markings yields a black-and-white striped foot corresponding to the position of the markings on the coronet. If the coronet is wholly white the hoof is without pigment ; it is frequently spoken of as 'white,' but it is really yellow. White hair only grows from a non-pigmented skin, and this condition constitutes albinism, so that white coronets and yellow feet indicate local albinism. Colourless feet are notoriously bad, and horses with white legs are, in consequence, generally disliked.

Face and Limb Markings.—Special attention has recently been drawn to the face and limb patterns produced by white hair in animals.* The face pattern may be symmetrical or one-sided, may cover the whole front and side of the face, and even involve the orbit. In this case the iris, sclerotic, and choroid partake of the non-pigmented condition, showing that this is not a mere accidental surface marking. Names have been given to face markings, but these need not concern us. Too much white on the face is a serious blemish, and a white muzzle with a pink skin is objectionable. In the paper referred to the writer states that the amount of white on the legs will be in ratio with the amount of white on the face. If the 'star' is not in the middle line, he considers there will probably be a want of bilateral symmetry in the markings of the limbs. He also points out that the hind-legs are almost always more extensively involved than the fore-legs, and that it is very rare to see white fore-legs only, and the hind-legs escape. Hutchinson considers that, where there is want of symmetry in the markings, as, for example, the face-patch to one side, or two lateral legs white and their fellows coloured, it may be suspected that the animal is not developed with perfect bilateral symmetry in other respects. He may be a 'left-handed' horse, and if so, though strong and efficient, will move awkwardly and be unpleasant to ride. We do not share this latter view, but the whole matter is so interesting and the facts so readily collected, that attention is drawn to our ignorance of the question, and the necessity for observation.

Albinism.—This is the absence of pigment from the skin, and may be general or local. Local albinism commonly affects the face and legs. It may be extremely local, as in *wall-eyed* horses, who possess no pigment in the iris of one or both eyes. It may affect the whole surface of the body, as in *white* (cream-coloured) horses with a pink skin ; or large areas of the bodies of such horses may be bay or black, and the remainder cream-coloured. In cream-coloured horses the choroid and iris are without pigment, the latter being bluish. A ' grey ' horse is not a ' white ' horse.

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* 'On Palæogenetic Face-Pattern in Acroteric Piebalds.' Sir Jonathan Hutchinson, F.R.C.S., F.R.S., *British Medical Journal*, June, 1910.

Clipping.—Experience shows that the heavy winter coat grown by horses is the cause of considerable sweating at work, and the general practice of clipping has hence been introduced. Of its value there can be no doubt ; it considerably reduces the risk of cold and chest diseases, for animals on coming in from work may be readily dried and thus protected from chills. Horses which sweat freely at work soon lose ' condition ' ; the writer's observations have shown that this is due to the protein lost by the skin, for, as we shall presently see, proteins are found regularly in the sweat of the horse. Clipping largely prevents this loss, though for this purpose it is not necessary to clip a horse all over ; a half-clipped body suffices. The influence of clipping on temperature is dealt with in the chapter devoted to Animal Heat.

Erection of Hairs.—In some animals, as, for instance, the dog and cat, the hairs are rendered erect under excitement such as anger or fear ; this is due to the involuntary muscle attached to the hair follicle, and the process is under the influence of the sympathetic nervous system. The fibres for the body-hair emerge from the spinal cord by the inferior roots, pass to the grey ramus of the sympathetic chain, and run to the skin by the dorsal cutaneous nerves ; the fibres for the head and neck are in the cervical sympathetic. Under the influence of cold the hairs on the horse's body may become erect, but there is no indication of this under psychical excitement, as in the case of the dog and cat. It is possible that the prescience of a coming storm or change of weather exhibited by cattle may probably be due to the highly hygroscopic properties of their hair. Hair is one of the few organic substances which elongate instead of shorten as they grow moist. The effect of movement of every hair on the surface of the body may cause a mechanical stimulation of the hair-follicle nerves, and so give rise to an uneasiness which presages the coming change.

Sweat.—By means of glands in the skin a fluid termed ' sweat,' and a fatty material known as ' sebum,' are secreted. Sweat, or perspiration, is not found to occur over the general surface of the body in any other hairy animal than the horse. There are certain parts of the skin which sweat more readily than others ; the base of the ears in the horse is the first place where sweating begins, the neck, side of chest, and back follow, lastly the hind-quarters. No sweating takes place on the legs ; the fluid found there has run down from the general surface of the body. Mules and donkeys sweat with difficulty, and then principally at the base of the ears. The ox sweats freely on the muzzle, and sweating even from the general surface of the body has occasionally been observed. It has been said that sheep perspire, while it is certain that both the dog and cat, especially the latter, sweat freely on the footpads, as also on the muzzle, though not on the general surface of the body. The sweating of the pig is confined to the snout.

The secretion of sweat is continuous. When excreted in small amounts it evaporates as fast as it is formed, passing off as the insensible vapour which is always rising from the surface of the skin, and is known as 'insensible perspiration.' When the secretion is rapid and copious or the surrounding atmospheric conditions are unfavourable to its evaporation, it collects on the skin as that visible fluid material which is ordinarily termed 'sweat.' Colin gives various numerical statements respecting the insensible perspiration, from which we gather that 6·4 kilogrammes (14 pounds) of water probably represent this loss in the horse for twenty-four hours. Much depends upon the humidity and temperature of the atmosphere; the drier and hotter it is, within certain limits, the greater the insensible perspiration.

The **amount of sweat** secreted daily can only be roughly determined; there are many conditions which affect it, such as the length of coat, nature of the work, and pace. Grandeau, by estimating the total water consumed in the food and drink, and that voided in the urine and fæces, arrived at the amount of vapour passing away in the breath and perspiration. The mean amount of water evaporated daily by these two channels, under different conditions of work, was as follows:

At rest - - - -	2·9	kilogrammes	(6·4 pounds).
Walking exercise - -	3·9	,,	(8·6 ,,).
At work walking - -	5·8	,,	(12·7 ,,).
Trotting - - - -	6·0	,,	(13·4 ,,).
At work trotting - -	9·4	,,	(20·6 ,,).

In each case the distance walked and trotted and the load drawn were the same. It is unfortunate that we have no means in the above experiments of determining the proportion which the water of respiration bears to that of perspiration.

Evaporation from the surface of the skin is a most important source of loss of heat; so marked is this in the horse that the resulting fall in temperature may even carry it below the normal, if the sweating be very profuse or the wetted area a large one.

The compensating action existing between the kidneys and skin observed in man exists also in the horse—viz., when the skin is acting freely less water passes by the kidney, and *vice versa.*

Sweat obtained from the horse is always strongly alkaline; after filtration it is the colour of sherry, which is probably accidental, and due to contamination with dandruff. The latter contains a pigment, chlorophyll. Sweat possesses a peculiar horse-like odour, and has a specific gravity of 1020. We found it to have the following composition:*

		Containing—	
Water - -	94·38		
Organic matters	0·52	Serum albumin - -	0·105
		,, globulin - -	0·327
		Fat - - - - -	0·002
Ash - - -	5·10	Consisting principally of potash and soda, chlorides, some magnesia, a little lime, and traces of phosphates.	

The proteins are thus seen to be serum albumin and globulin, and their constant presence has been determined by a number of observations; the mineral matter is very high and consists principally of soda and potash, especially the latter. It will be observed that the mineral matter greatly exceeds the organic matter; in horses which have sweated freely the dried, matted hair (which is due to albumin) is often seen covered with saline material, looking like fine sand. There appears to be some complemental action between the skin and the kidneys in the elimination of soda and potash; during rest the kidneys eliminate these salts, while during work they are assisted by the skin. Urea is also probably present in sweat (see p. 311). It is difficult to see why horses should excrete albumin by the skin; the loss thus produced accounts for the great reduction of vitality and strength in animals which sweat freely at work, and for which clipping is the only preventive.

Nervous Mechanism of Sweating.—A skin may sweat under quite opposite conditions—viz., both with a hot flushed skin and a bloodless cold skin; in other words, an animal may sweat when it is hot or when it is cold. The former is a physiological condition and regulates, as we shall see, the body temperature; the latter is abnormal, but it occurs and disproves at once any notion of sweating necessarily depending upon a congested condition of the vessels of the skin. Experiments show that most of the features of sweating can be accounted for through the agency of the nervous system. Though we are ignorant of the manner in which the nerves terminate in the sweat glands, still, it is certain that there are special branches of nerves, whose function it is to determine the secretion of sweat, and these are quite distinct from those which regulate the vascular supply. If the peripheral end of the divided sciatic in the cat be stimulated, the foot-pads sweat; the proof that this reaction is a specifically nervous one is easy, apart from the fact that stimulation of the sciatic causes a violent constriction of the bloodvessels in the leg, for the sweating occurs when the leg has been cut off or the aorta tied, and it is absent under the influence of atropine. The effect of atropine on the sweat glands is very closely allied to its action on the salivary glands (p. 169); it paralyses the secretory nerves which produce sweat.

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* 'The Sweat of the Horse,' *Journal of Physiology*, vol. xi., 1890.

As with the salivary glands, so in the present case secretion is not due to any increased supply of blood. It is true that in normal sweating, as is so readily seen in man, the skin is flushed as the increased secretion takes place, but the increased blood-supply which the flushing indicates is merely the necessary adjuvant, not the cause of the secretion; it supplies the glands with the extra material they now require, the secretory nerves causing the gland-cells to utilise the increased supply.

The secretion of sweat may be induced in man, the cat, and the dog, though not in the horse, by the injection of pilocarpine. In this case the action is peripheral—that is to say, on the glands themselves—since it occurs when the sciatic nerves are cut previously to the injection.

As we have seen, secretion is ordinarily brought about by specific efferent nerves, and these originate in the central nervous system, from which the necessary secretory impulses are directly supplied. But secretion may also be readily induced by the stimulation of *afferent* nerves, as in the all-important case of a rise in the surrounding temperature. These facts lead at once to the belief that 'sweat centres' must exist in the central nervous system comparable to those of the respiratory and vascular mechanisms, though they have not as yet been so definitely localised. There seems to be no doubt that the spinal cord contains sweat centres. The existence of a similar centre in the medulla is less certain, though probable, since in some men perspiration over the face and neck results from merely smelling a pungent substance, such as curry-powder, and becomes profuse if the latter is introduced into the mouth.

The sweat-nerve supply to the fore and hind limbs leaves the spinal cord in company with the inferior roots of the spinal nerves, and by means of the *rami communicantes* passes to the sympathetic ganglia, and by post-ganglionic fibres reaches the brachial and sciatic plexuses respectively. The sweat fibres for the head and neck are in the cervical sympathetic; those for the face in the horse, the muzzle in the ox, the snout in the pig, run in branches of the fifth pair of nerves. Division of the cervical sympathetic in the horse produces profuse sweating of the head and neck, limited to the side operated upon; this may be due to vaso-motor paralysis, though a different interpretation has been placed on it—viz., that the sympathetic carries inhibitory impulses to the sweat glands of the head, so that on division the secretory fibres act without opposition. In the ox Arloing has shown that division of the cervical sympathetic causes the muzzle on the same side to become dry; stimulation of the cut end of the nerve is followed by secretion, but this is not so when the nerve degenerates, though even then the glands respond to pilocarpine.

As previously stated, a high temperature favours the activity of the epithelium lining the sweat glands, for if the limb of a cat be kept warm, a larger secretion of sweat is obtained on stimulating the sciatic than in a limb kept cool; in the latter stimulation of the sciatic may produce no secretion whatever. Further, if a cat in which one sciatic has been divided be placed in a hot chamber, profuse secretion will occur on the foot-pads of the limbs not subjected to interference, while on the side on which the sciatic has been divided no sweating occurs. This is a further proof of the existence of a reflex mechanism, to which we have already drawn attention. It has been thought that the sweating which takes place at death is due to a dyspnœic condition of the blood, and in many cases this may be so; perhaps it may also account for the profuse cold sweating in ruptures of such viscera as the stomach and intestines; but it cannot explain the localised hot sweating which is often so well marked in horses between the thighs immediately after they are destroyed. Thrombosis of both iliac arteries may occur in the horse, and a frequent symptom of this trouble is the peculiarity in the accompanying sweating; the general surface of the body may sweat freely, but not the hind-quarters. In man a similar phenomenon has been met with in cases of spinal injury. The cause of this peculiarity has not been worked out.

In comparing the sweat glands with the salivary, we must be careful not to draw too close a parallel, for though in certain features they agree, in others they are very different; for instance, in the horse pilocarpine produces, as in other animals, a profuse salivary flow, but, unlike its action on man, the dog, and cat, it has no effect whatever in producing sweating.

The peculiar breaking out into sweats which occurs in horses *after* work has no parallel in man; some animals will break out two and three times for hours afterwards, even after having been rubbed quite dry. This may be connected with the necessity for a discharge of body-heat, since the internal temperature rises above the normal during work, in some cases, it is said, as much as 2·5° to 3° C. (4° to 5° Fahr.), and remains so for some time afterwards. Another peculiarity in sweating of the horse is the patchy perspiration observed occasionally, such as a wet patch on the side or quarter which dries slowly, or may remain for days or weeks, even months, in a wet or damp condition. This must be a paralytic secretion, but nothing is known of its true nature. Finally, there is no drug, so far as we are aware, which produces sweating in horses ; this is perhaps an explanation of the common use of nitre in veterinary practice, the kidneys being made to do the work of the skin.

Sebaceous Secretion, or **Sebum,** is a fatty material formed in the sebaceous glands of the skin, which in the horse are freely distributed over the whole surface of the body. Though it is spoken of as a secretion, yet the process involved is not secretory, inasmuch as the cellular elements of the gland are not actively employed pouring out material, but are themselves shed after undergoing fatty metamorphosis. The greasy material thus produced saves the epithelium from the disintegrating influence of wet, keeps the skin supple, and gives the gloss to the groomed coat ; from its greasy nature it assists in preventing the penetration of rain, and thereby saves, to some extent, undue loss of heat.

Dandruff.—The material removed from horses by grooming consists of a white or grey powder which can readily be moulded by pressure into a dough-like mass ; it has a curious smell, which can only be described as 'horse-like.' It consists of epithelial scales, fat, largely in the form of lanolin, colouring matter, salts, and a considerable amount of silica and dirt, the two latter depending upon the cleanliness of the animal. The amount of dandruff lost in an ordinary grooming varies from 1·25 to 3·75 grammes (20 to 60 grains) for clean horses, and 11 to 13 grammes (170 to 200 grains) for very dirty animals. An analysis of dandruff from the horse gave the following composition :*

Water - - -	17·96	
Fat - - - -	12·40	
Organic matter -	56·22	containing 1·07 of urea.
Ash - - - -	13·42	,, 2·45 of silica.
	100·00	

The fatty matter in the skin proves to be lanolin, the same as that found in the fleece of sheep ; it explains the reason why horses living in the open should not be too freely groomed, and supports the prejudice which has always existed against this practice. It is evident that with free grooming the loss in fat alone is something considerable, and the animal exposed to chill. The amount of fat depends upon the nature of the diet; on a purely hay diet there is very little fat in the dandruff, while on oats there is a considerable amount. The urea shown in the analysis is no doubt derived from the sweat.

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* 'Dandruff from the Horse, and its Pigment,' *Journal of Physiology*, vol. xv., 1893.

Dandruff contains a colouring matter found by the writer to be chlorophyll which has undergone modification by passing from the digestive canal to the skin. The use of this pigment is unknown; in fact, the horse is the only vertebrate in which chlorophyll has so far been found as a constituent of any cutaneous excretion.

In certain places, as in the prepuce, considerable quantities of **sebum** are found. The sebaceous secretion of the prepuce of the horse consists of 50 per cent. fat, and also contains calcium oxalate. The ear-wax and eyelid secretions are also of a sebaceous nature. In the sheep a considerable quantity of fatty substance is found in the wool; it exists in two forms, (1) as a fatty acid united to potash to form a soap, and (2) a fatty acid combined with cholesterin instead of glycerin; the latter is known as lanolin, and is largely used as a basis for ointments. It is also found in hair, horn, feathers, etc. The fatty substance in the wool is known to shepherds and others as 'suint.' In merino sheep it may amount to more than one-half the weight of the unwashed fleece, but in ordinary weather-exposed sheep it may be 15 per cent. or less. The large amount of potash in unwashed wool is very remarkable; a fleece sometimes contains more potash than the whole body of the shorn sheep (Warrington).

Respiratory Function of the Skin.—Certain vertebrates such as the frog can respire by the skin in the entire absence of lungs; in this way they absorb oxygen and excrete carbonic acid. Observations made on animals and men have demonstrated that similar changes occur through the skin, but on a very small scale.

Varnishing the skin rapidly causes death in rabbits, and more slowly in horses. Death is due to loss of body-heat, and not to the retention of poisonous products, as was at one time supposed. Bouley* states that horses shiver when varnished, and the surface of the body and the expired air become colder, the visible membranes respond by becoming violet in tint, and the animals die after several days. According to Ellenberger, if only partly varnished they do not die, but exhibit temporary loss of temperature, and show signs of weakness. The effect of varnishing the skin is to cause the capillaries to dilate, and so produce a great discharge of heat.

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* Colin's 'Physiologie Comparée.'

For absorption from the skin, see ' Absorption,' p. 282.

The **Chestnuts** and **Ergots** are considered to be the remains of hoofs belonging to digits long since lost by the horse ; the former can be distinctly seen in the fœtus. The ergot grows from the back of the fetlock ; the chestnut is found on the inside of the arms and hocks, and is always larger in the former position. In the heavy type of horse it may grow to a considerable size. The horn of which it is composed is tubular in structure, and produced by the papillæ of the skin. After growing a certain size they drop or are pulled off. Both ergots and chestnuts are found larger in horses wanting in quality than in those better bred ; in the donkey and mule the chestnut forms no outgrowth of horn, but a hairless black patch represents its position.

Pathological.

The chief pathological conditions of the skin are those due to parasitic invasion ; this may produce widespread disease in all animals.

CHAPTER X

THE URINE

THE urine is sometimes spoken of as a secretion, but this is not strictly correct ; speaking broadly, it may be said that a secretion is something which is formed in a part for the purpose of being eventually utilised by the system. This does not apply to the urine, the chief constituents of which are not even prepared in the kidneys, but only separated by them ; moreover, the urine having once been formed is of no further use to the body, and is excreted. An excretion, therefore, is something removed from the system as being no longer required, and the retention of which would be harmful. Such a removal is effected by the kidneys, which may in a sense be regarded as the filters of the body, regulating the composition of the blood by removing from it waste and poisonous products, and maintaining, as will be later explained, its proper degree of chemical neutrality.

The method adopted by the kidney for the secretion of urine has been for many years one of the chief fields for physiological dispute. A pair of very vascular glands are capable of removing from the blood a fluid which is essentially different in composition to the blood itself. The blood is neutral in reaction, the urine acid or alkaline, depending on the class of animal ; the blood is a proteic fluid, the urine in a state of health is free from protein ; the blood contains sugar, the urine contains none ; the blood has one colouring matter, the urine another ; the blood contains urea and salts in small quantities, the urine contains them in relatively large amounts ; the blood maintains the whole of its inorganic material in solution or packed away in such a form as to be readily soluble, the urine may be of such concentration or reaction as to be unable to retain its substances in solution. Nevertheless, the kidney only takes from the blood what is brought to it, for, with the single exception of hippuric acid, none of the other urinary constituents are formed in the gland. There is no other body-secretion which exhibits these striking differences, and, further, there is no other gland which resembles the peculiar histological structure of the kidney.

The vascular arrangements of the kidney are intimately connected with the function of the organ. The renal artery is short, it comes off close to the posterior aorta, and the pressure within it is practically the pressure in that vessel; the pressure in the renal vein, on the other hand, is low, nearly as low as that in the posterior vena cava. It will be observed that the same amount of blood-pressure as is required to fill the vessels of the lumbar region and hind-limbs is expended on driving the blood through the kidneys. At every increase in the amount of blood in the kidney the organ swells, at every decrease it contracts. These movements on the part of the kidney have been carefully studied by means of Roy's *oncometer*. An oncometer (Fig. 92) is a metallic capsule in which the living kidney is enclosed, and so arranged that the expansion and collapse of the organ can readily be recorded. A tracing given by the use of this instrument shows that the volume of the kidney is affected by every beat of the heart, and even by the respiratory undulations in the blood-pressure.

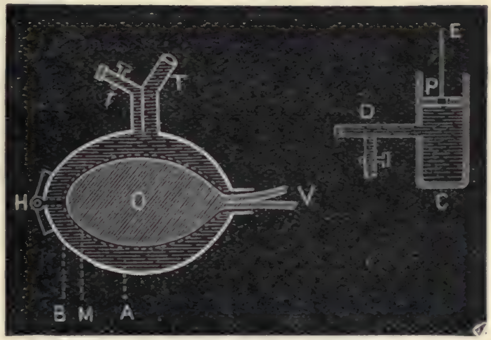


FIG. 92.—DIAGRAM OF ONCOMETER.

B, Metal box in two halves, opening on the hinge H; M, thin membrane; A, space filled with oil; O, organ enclosed in oncometer; V, vessels of organ; *t*, tube for filling instrument with oil; T, tube connected with D, which opens into cylinder C; P, piston attached by E to writing lever.

Structure of the Kidney.—The kidney consists of a central part, the medulla, surrounded by an external part, the cortex; the boundary of the two is easily visible in a sliced kidney. The branches of the renal artery break up at the boundary of the cortical and medullary portions. The cortex of the kidney is the essential secreting region, and it is here that the *Malpighian tufts* or *capsules* are found. These consist of small balls of capillaries, the *glomeruli*, derived from the renal artery; the artery entering the Malpighian tuft is larger than the vein leaving it, the result is that a high blood-pressure is maintained in the glomerulus. The vessel which supplies these tufts also sends branches to form a plexus around the *uriniferous tubules;* these branches do not enter the Malpighian body. The whole glomerulus is contained in a capsule in which it is suspended by its afferent and efferent vessel; when the vessels are dilated the tuft fills the capsule, when they are collapsed there is a space between them. Fig. 93 shows the general arrangement of the Malpighian bodies, and Fig. 94 that of the vessels in the tuft. The minute vein or efferent vessel leaving the tuft breaks up into capillaries around the uriniferous tubule; thus the blood in the plexus of capillaries around the tubule is derived from two sources—viz., from the tuft, and directly from the renal artery. The capsule of Bowman, which surrounds the tuft, is lined by cells resembling the epithelioid plates seen in capillaries; they are flat polygonal cells containing a nucleus. The capsule is practically the dilated beginning of a uriniferous tubule, and

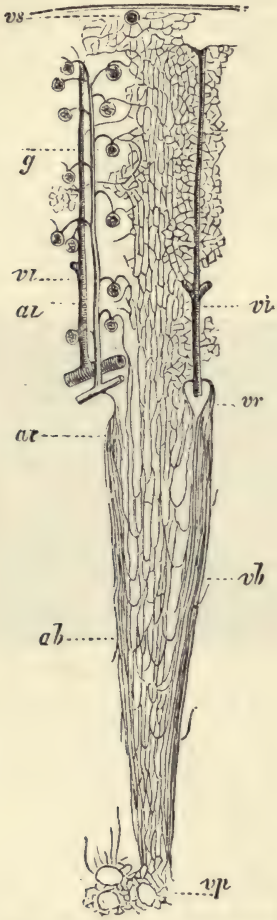


FIG. 93.—DIAGRAM OF BLOODVESSELS OF KIDNEY (KLEIN, AFTER LUDWIG).

ai, Interlobular artery; *vi*, interlobular vein; *g*, glomerulus with its afferent and efferent vessels, the latter breaking up into a plexus around the renal tubules; *vb*, venæ rectæ; *ar*, arteriæ rectæ; *vp*, apex of papilla; *vs*, vena stellata (Stewart).

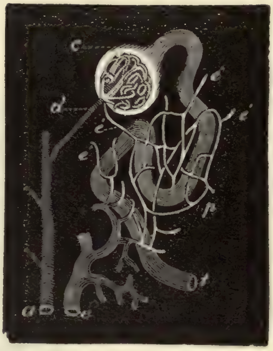


FIG. 94.—DIAGRAM SHOWING THE RELATION OF THE MALPIGHIAN BODY TO THE URINIFEROUS TUBULES AND BLOODVESSELS (KIRKE, AFTER BOWMAN).

a, An interlobular artery; *a'*, branch of artery passing into the glomerulus; *c*, capsule of the Malpighian body forming the commencement of, and continuous with *t*, the uriniferous tube; *e'e'e'*, vessels leaving the tuft forming a plexus, *p*, around the tube, and finally terminating in *e*, a branch of the renal vein.

the latter is continued from the capsule, taking a course of extraordinary complexity in order to reach the pelvis of the kidney; further, the cells found in the tubule are no longer the flat polygonal cells of the capsule, but a something special to the tubule, and even to different parts of it (Fig. 95).

If the course of a uriniferous tubule is briefly followed (Fig. 96), it is found that on leaving the capsule it becomes twisted in the cortex forming the *convoluted tube;* it then forms a *spiral tube,* and leaving the cortex, runs straight into the medulla, forming the *descending limb of Henle;* it now makes a sharp turn, the *loop of Henle,* and travels back to the cortex, in the same way that it left, by the *ascending limb of Henle.* The descending limb is straight and narrow, the ascending limb is wavy in character and larger. Having reached the cortex, the ascending limb becomes distinctly wider and twisted, forming the *zigzag* or *irregular tubule;* from this a tubule is continued which resembles in its contortions the first convoluted portion; it is termed the *second convoluted tubule.* This now leaves the cortex and enters the medulla as a straight tube, known as the *collecting*

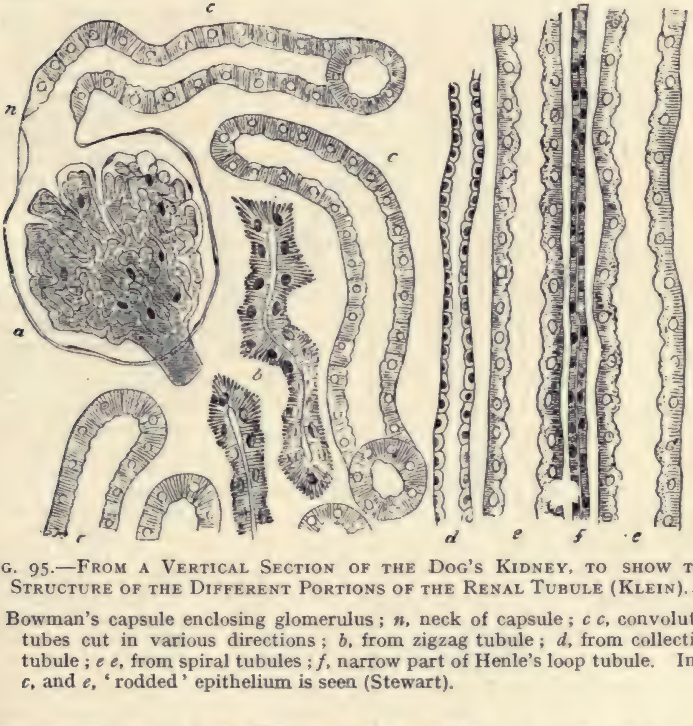
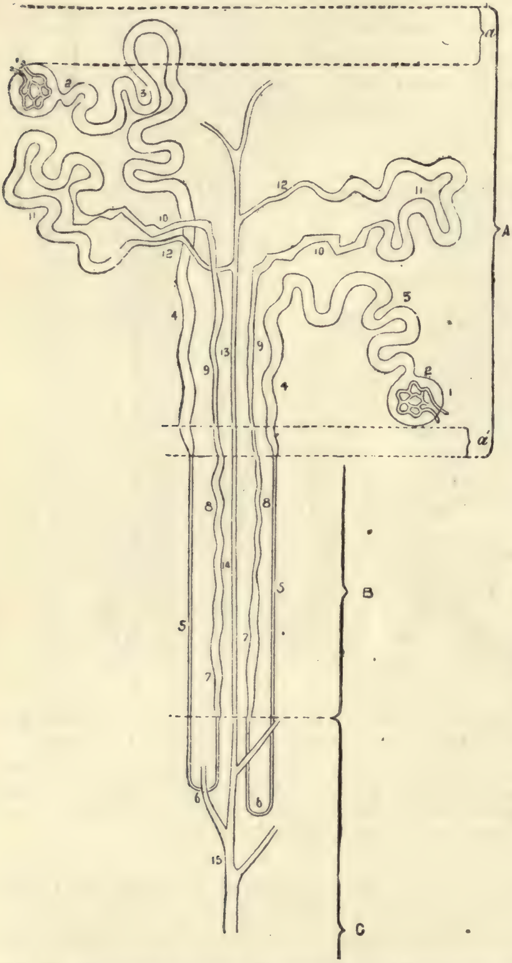


FIG. 95.—FROM A VERTICAL SECTION OF THE DOG'S KIDNEY, TO SHOW THE STRUCTURE OF THE DIFFERENT PORTIONS OF THE RENAL TUBULE (KLEIN).

a, Bowman's capsule enclosing glomerulus; ***n***, neck of capsule; ***c c***, convoluted tubes cut in various directions; ***b***, from zigzag tubule; ***d***, from collecting tubule; ***e e***, from spiral tubules; ***f***, narrow part of Henle's loop tubule. In ***b***, ***c***, and ***e***, 'rodded' epithelium is seen (Stewart).

tube ; it runs towards the apex of the pyramid and joins other collecting tubes ; by so doing it becomes larger, and on reaching the apex, is known as a *discharging tube* or *duct of Bellini.* The epithelial cells lining the tubules are not of the same character throughout ; broadly, they may be divided into a striated or 'rodded' cell staining readily, and a clear transparent cell staining with difficulty. The 'rodded' epithelium is suggestive of secreting cells, and is found in the two convoluted tubules,



A. Cortex of kidney ; *a*, subcapsular layer not containing glomeruli ; *a'*, inner structure of cortex also without glomeruli ; B, boundary layer of medulla ; C, papillary part of the medullary ; 1, Bowman's capsule of the glomerulus ; 2, neck of capsule ; 3, proximal convoluted tube ; 4, spiral tube ; 5, descending limb of Henle ; 6, loop of Henle ; 7, thick part of ascending limb ; 8, spiral part of ascending limb ; 9, narrow ascending limb in the medullary ray ; 10, the irregular tubule ; 11, distal convoluted tube ; 12, curved collecting tube ; 13, straight collecting tube ; 14, collecting tube of boundary layer ; 15, large collecting or discharging tubule of papillary layer.

FIG. 96.—DIAGRAM OF THE COURSE OF THE URINIFEROUS TUBULES (KLEIN AND NOBLE SMITH).

spiral and zigzag tubules (Fig. 95); the clear cell, on the other hand, possesses more the characteristics of the epithelial lining of ducts.

Vascular Mechanism.—The vascular arrangements of the kidney are under the control of a rich supply of vaso-constrictor nerves, while dilator nerves are also known to exist. If the general blood-pressure be constant, dilatation of the renal vessels means an increased secretion of urine, while constriction of the vessels means a reduced secretion. An increase in the general blood-pressure produces an increase in the amount of blood in the kidney, and this is rendered evident by the swelling of the organ in the oncometer and an increased production of urine. If the increased general blood-pressure is accompanied by a *constriction* instead of a dilatation of the small arteries of the kidney, such, for instance, as when the vaso-constrictor nerves are stimulated, then the increased blood-pressure cannot lead to increased secretion, but, on the contrary, the amount of urine becomes less and the kidney *shrinks*. A fall in general blood-pressure, such as is caused by dividing the spinal cord, brings about a reduction in the flow through the kidney, and the blood-pressure becomes so low that the secretion of urine is entirely suspended. It is thus evident that the vasomotor influence over the kidney is of the greatest importance, and largely regulates the amount of urine manufactured. If the renal vein be obstructed, the pressure of blood in the kidney rises, but no urine is secreted; evidently, therefore, an increased flow of blood through the kidney is as essential to secretion as is increased blood-pressure.

The **Theories of Urinary Secretion** are two in number. One put forward by Bowman regarded the epithelium of the glomerulus as the seat of secretion of the water and inorganic salts of the urine, while in the convoluted tubules the epithelium secreted the urea and other organic substances. The view is essentially secretory, and is opposed to the other formulated by Ludwig, which is essentially mechanical in character. Ludwig regarded the glomerulus as the seat of formation of the entire urinary constituents under the influence of pressure brought about by the peculiar structural arrangements of the part. In the glomerulus, according to this view, a highly diluted fluid was formed which, in its passage to the pelvis of the kidney, was exposed to *absorption* by the epithelial cells, by which means it became concentrated. The majority of physiologists accept the Bowman theory.

If the whole process of urinary secretion were a question of pressure in the glomerulus, then ligature of the renal vein should result immediately, though not continuously, in a greater secretion of urine. As a matter of fact, we know the secretion ceases. This experiment is a very crucial one. The fact of closing the venous outlet must greatly raise the capillary pressure, and favour in a remarkable manner the passage of fluid by filtration, yet none is filtered off. Many experiments have been made to prove the secretory activity of the cells of the convoluted tubes; the one by Heidenhain is generally regarded as conclusive.

If sulphindigotate of soda be injected into the blood of the dog, within a short time the urine acquires an intensely blue colour, though the blood may be only slightly affected. If the kidney be removed and examined, all parts excepting the Malpighian bodies are found stained blue. In order to determine what portion of the tubule excretes the dye, it is necessary to stop the secretion in the glomeruli, otherwise the colouring matter gets carried through the whole length of the tubule. In order to stop glomerular secretion, the blood-pressure is lowered by dividing the spinal cord in the neck, and the blue colouring matter is then injected, and the kidney subsequently examined. The blue is now found in the cortex only, and within the striated or rodded epithelial cells of the first and second convoluted tubes, in which the pigment may be seen lying in granules. From this experiment it is clear that the cortical tubules elected to turn out the pigment from the blood, while the medullary tubules were unable to effect this. It is therefore fair to assume that a specific secretory activity of the cells of the convoluted tubes is shown for indigo, and it is assumed that a similar function may be exercised towards other bodies—for instance, urea and the other constituents of the urine.

Stating these points briefly in connection with secretion, they amount to this, that in the glomeruli the water of the urine, and perhaps the salts, are passed out chiefly as the result of varying glomerular blood-pressure, while in the tubules the organic matter is excreted as the result of a distinctly secretory activity of their cells. These substances are carried along by the fluid which trickles down the tubules into the pelvis of the kidney, and so becomes urine. The secretion of protein in the tuft, and its reabsorption in the tubule, was at one time believed to be true, but inasmuch as no protein is found in the normal urine of any animal, it is safe to assume that in an undamaged state the epithelial cells of the glomerulus allow none to pass. Under pathological conditions the glomeruli admit of the exit of both albumin and sugar. There are no secretory nerves to the kidney; the influence of the nervous system is confined to its action on the bloodvessels, and so regulating the flow of blood through the kidney.

The latest view of urinary secretion is that put forward by Brodie.* He regards the glomerular activity as secretory, and considers that the high blood-pressure in the glomerulus is the propelling force which drives the urine secreted by the tubules through their very long and narrow passage. He proposes to call the glomerulus a ' propulsor,' and points out that the kidney during activity is tense, hard, and distends its capsule to the utmost, which he considers is explained on the basis of the propulsor theory. The importance of a firm inextensible capsule to the kidney has not previously been insisted upon.

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* 'Glomerular Activity,' Proceedings of the Royal Society, June 15, 1911. Dr. T. G. Brodie, F.R.S.

The action of diuretics has been studied in connection with the question of urinary secretion, and the general outcome of the work is that these effect their purpose either by increasing the flow of blood to the kidneys, or by directly stimulating the secretory activity of the cells.

The function of the cells of the tubules does not end with the removal from the blood of the substances presented to them; they are also capable of originating material on their own account. Thus the union of glycine with benzoic acid, resulting in the formation of hippuric acid, takes place in the cells of the tubules, and observations have shown that, providing the benzoic acid be presented to it, the kidney is capable of providing the needful glycine. It can hardly be doubted that what is true of glycine and benzoic acid may also be true of other substances, and that transformations may occur in the cells leading to the production of colouring matters, etc., our knowledge of which is at present obscure.

The **Composition of the Urine** depends upon the class of animal; in all herbivora, with certain minor differences, the urinary secretion is much the same: not so with omnivora or carnivora, which possess a distinctive urine, especially the latter. When herbivora live on their own tissues, as during starvation, they become carnivora, and their urine alters completely in character, corresponding now to the urine of flesh-feeders; the young of herbivora, if still sucking, have a urine possessing much the same characteristics as that of carnivora. But apart from this general statement, it is necessary to point out that in animals of the same class the composition of the urine may vary within very wide limits, depending upon several causes, of which diet is, perhaps, the most important.

Urine consists of—

Water.	
Organic matter -	Nitrogenous end-products: urea, uric acid, hippuric acid, kreatin, kreatinine. Aromatic compounds: benzoic acid, ethereal sulphates of phenol, cresol, etc. Colouring matter and mucus.
Salts - -	Sulphates, phosphates and chlorides of sodium, potassium, calcium, and magnesium.

The **Nitrogenous Substances** taken up into the blood, either from the disintegration of proteins in the digestive canal or from the metabolism of the tissues, supply the total nitrogen of the urine. A distinction is made between the nitrogen in urine, which results from the breaking down of the food in the intestinal canal and the nitrogen from within—viz., that furnished to the urine by the metabolism of the body tissues—and this is more especially of interest in connection with urea and uric acid.

The total nitrogen of the urine consists of—

1. *Urea nitrogen.*
2. *Uric acid nitrogen.*
3. *Ammonia nitrogen.*
4. *Kreatinine nitrogen.*

Urea, or carbamide, is the substance in urine which represents the form in which the greater part of the nitrogen is got rid of: 1 gramme of protein yields $\frac{1}{3}$ gramme of urea. It is a substance very soluble in water, crystallises readily, the crystals melting on heating, and giving off ammonia. In the urine it exists in a free condition, but is capable of forming salts with acids. These yield typical crystalline formations, by which they can be identified microscopically, such as octahedra, with nitric acid (see Fig. 97). Under the influence of a ferment, the *Micrococcus ureæ*, urine, on standing, becomes ammoniacal, due to the breaking up of the urea into ammonium carbonate. This also sometimes occurs in the bladder under pathological conditions. Urea is found in blood in proportions which vary between 4 and 6 per 10,000; in the urine it exists in the proportion of 300 parts per 10,000. It is only by the constant flushing of the kidneys with blood that this amount of urea is separated, and the size of the stream may be judged by the fact that a dog weighing 35 kilogrammes (77 pounds) has 300 kilogrammes (660 pounds) of blood streaming through the kidneys every twenty-four hours. The peculiar selective power of the kidney cells cannot be better exemplified than in the matter of urea. The cells of

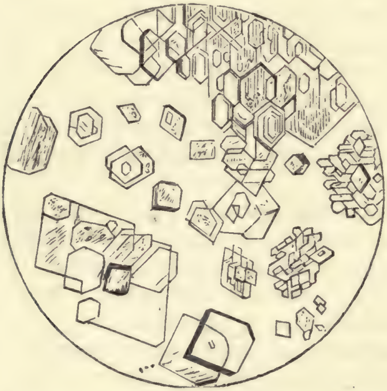

FIG. 97.—CRYSTALS OF NITRATE OF UREA.

the tubules pick it out from the blood in spite of its high dilution in that fluid, and reject sugar, which is sixteen times as much.

It is evident that the disintegration of protein material which leads to the formation of urea may be occurring in the actual protein of the tissues (*endogenous* production), or it may be taking place in the protein substances absorbed from the intestinal canal which are not part of the tissues. This is known as *exogenous* production. It is not possible to say exactly how much is contributed from each source, but it would seem that the major portion is furnished from the protein food substances not built into the protein of the tissues.

The history of urea is still very incomplete, but it is now generally accepted that it is formed, though perhaps not exclusively, in the liver, and that the kidneys are only its path of excretion. The form in which the antecedents of urea arrive at the liver is not definitely known, nor, indeed, are the various stages existing between protein and urea agreed upon. We have seen (pp. 189, 255) that the protein molecule, under the influence of pepsin, trypsin, and erepsin, is gradually reduced from complexity to simplicity, and in so doing its nitrogen appears as ammonia, monamino-acids, and diamino-acids. There is no reason to doubt that what occurs in the intestinal area in the breaking up of the protein molecule may also occur in the tissues. Muscles, for instance, contain ammonia in large quantities. Ammonia is formed in the body tissues by intracellular ferments, and is carried by the blood to the liver. The form in which it is carried is not agreed upon, but as the ammonia in the tissues unites with carbon dioxide, it is probably carried either as ammonium carbamate or carbonate. In the liver the conversion of this into urea by the loss of a molecule of water is easy to understand. If the blood of the portal vein be experimentally compelled to pass into the posterior vena cava without circulating through the liver, the output of urea is decreased, while the ammonia compounds increase in the blood and cause poisoning. The blood of the portal vein is found to contain three or four times more ammonia compounds than arterial blood, and there can be no doubt that these highly poisonous compounds are converted in the liver into the less poisonous urea. It is well known that monamino-acids, resulting from protein disintegration, such as *leucine*, *glycine*, and *aspartic acids*, may be converted into urea, and it is most likely that this change is effected during their passage through the liver. The diamino-acids, represented in the body by *histidine*, *lysine*, and *arginine*, are also capable of conversion into urea. Arginine, for example, is acted upon by the ferment *arginase*, which is found in the liver, kidneys, and other organs, and converted into urea and ornithine. No arginase is found in muscle.

The largest part of the urea excreted is not produced by the metabolism of tissue protein, but from the products of food absorption, and these are mainly represented by the ammonia compounds taken up from the intestinal area. The urea contribution effected by the tissues may also be represented by ammonia compounds and monamino-acids, but probably more especially by the splitting up of arginine. Uric acid has been considered by some physiologists as a possible source of urea, for it has been observed in man that about one-half of the uric acid produced is not excreted as such, but is got rid of as urea; in dogs, however, only one-twentieth undergoes this conversion. This change is effected by a uricolytic ferment found in the liver and other organs. Uric acid given by the mouth is excreted as urea, and outside the body it is readily converted into urea by oxidation; nevertheless, this is not very strong evidence in favour of the existence of uric acid conversion in the living body. Kreatinine was at one time regarded as a source of urea, but with a better knowledge of this substance and kreatin, the conversion of kreatinine into urea, which offers no difficulty as a laboratory process, is regarded in the living body as doubtful.

There is one remaining source of urea to be glanced at, and that is the urea which is supposed to be capable of manufacture in the tissues. It has been found that when the liver is removed urea does not disappear from the urine, and it is supposed that the origin of this portion is from the tissues, though not necessarily formed in the same way as the liver-urea, nor from the same material.

The proportion of urea in urine varies dependently on the nature of the diet. In man and the dog the larger the amount of nitrogen in the food the more urea excreted, but in herbivora it has been observed that on a diet consisting principally of hay more urea is excreted than on one of oats and hay. Urea was at one time considered to be a measure of the amount of work performed by the animal body, but this view has long been known to be wrong, though there can be no doubt that under the influence of work rather more urea may be excreted than during rest.

Apart from these marked causes of variation there are others, which certainly in the case of the horse lead to great differences in the daily excretion, even under identical conditions, of work, food, and rest. We shall see also that this is so in the dog, an animal in which the widest variations occur in the urea. In the horse, about 100 grammes (3½ ounces) daily is a mean excretion; that for other animals will be given elsewhere (pp. 338, 339). The percentage of any substance in urine conveys no information unless the total amount of excretion for the twenty-four hours has been ascertained. Nevertheless, it is usual to speak of the percentage of urea and other substances, and it is a useful expression if the other data be known. In the horse the urea may vary from 2·5 to 4 per cent.

Kreatin and **Kreatinine** are found largely in muscular tissue, and the amount may be doubled by severe exercise or prolonged starvation. The facility with which kreatin can be converted into urea by boiling with an alkali, suggested that in the body it might be a source of this substance. This is now known to be incorrect. If administered to dogs by the mouth, it is excreted, not as urea, but as kreatinine. In rabbits, as representing herbivora, only a minute portion is recovered as kreatinine, the remainder cannot be recovered in any form.

The kreatin story is far from known. Some consider that the kreatin of muscle is not converted into the kreatinine of urine, but that kreatinine is, in all probability, formed in the liver in the course of protein metabolism; from there it is passed to the muscles, where it is stored as kreatin, and the excess got rid of by the kidneys as kreatinine. In flesh feeders a portion of the urinary kreatinine is derived from the food, but this substance continues to be excreted on a meat-free diet, while if a diet be given in which the proteins are reduced in amount, the kreatinine is increased. In the human subject it is found that, though the amount of kreatinine naturally varies in different people, yet it is constant for the individual. So marked is this, that it can be employed as a check on the total amount of urine secreted. The source of kreatinine is unknown. It is suggested that the conversion of kreatin into kreatinine in the body is due to a ferment, but no definite statement can at present be made regarding either of these substances. Next to urea and the ammonia compounds, kreatinine forms the most important nitrogenous substance in the urine.

Uric Acid.—This is the chief end-product of protein metabolism in birds and reptiles. It is manufactured in the liver by synthesis from ammonia and lactic acid, and excreted as acid ammonium urate. In contrast to urea, it is a very insoluble substance in water, but is soluble in alkaline solutions and in alkaline phosphates. With the latter an acid urate of the alkali is formed, and acid sodium phosphate results, which gives the reaction to the urine of the carnivora. In the mammal it is known that the chief source of uric acid is not by synthesis as in the bird, but by the splitting up and oxidation of a special group of protein substances known as nucleo-proteins. These bodies may be derived from the food, or from the tissues, as we have seen is the case with urea. In man food rich in nuclein, such as thymus, pancreas, and herring roe, and in purin bases as meat extract, increases the amount of uric acid produced. Uric acid (Fig. 98) does not exist in the urine in a free state, but as urates of soda or potash. Two classes of urates are formed—normal and acid. The acid sodium urate is the chief constituent of the reddish deposit of urates which occurs in acid urines.

We have referred to **purin** bases as bodies, and a word in explanation is necessary. Purin is the name given by E. Fischer to the nucleus common to the uric acid group of substances, from which, by transformations, several members of the group may easily be obtained.

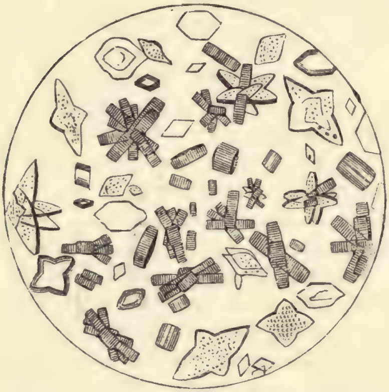

Fig. 98.—Crystals of Uric Acid (Funke).

The purin group consists of the following bases:

Purin Bases. {
Xanthine.
Hypoxanthine.
Adenine.
Guanine.

And from these uric acid may be formed probably by the following process: Under the influence of ferments the nuclein is split off from the protein and acted upon by a tissue enzyme known as nuclease. This splits the nuclein, and results in the formation of the above-named purin bases. Adenine and guanine, under the influence of ferments, are converted into hypoxanthine and xanthine, and these bodies, on being acted upon by an *oxidase* ferment, are oxidised to uric acid.

Of the uric acid so formed a portion under the influence of a urolytic ferment is, as previously noted, converted into urea.

The uric acid problems have been worked out mainly on the dog, apart from what has been done on birds. In the case of the non-suckling herbivora, it is known that in a condition of health uric acid is not found, or only to a trifling extent. It is present in the suckling, also in the adult, immediately the animal begins to live on its own tissues, as in disease. It appears clear that a flesh diet, especially of cellular organs such as the various glands, favours its production, while a vegetable one either inhibits its formation or else destroys it, perhaps in the liver, under the influence of a body ferment, and urea produced. This is pure conjecture. The question of the production of uric acid in vegetable feeders has not, as far as we know, been worked at, though its physiological interest is considerable.

Hippuric Acid.—This acid is characteristic of the urine of the herbivora; traces may also be found in the urine of man, but none in birds. Hippuric acid cannot be detected in the blood, nor does it exist free in the urine, but as hippurates of lime or potash, probably the former (Figs. 99, 100). Chemically it is a conjugated acid formed by the union of glycine with benzoic acid. The synthesis takes place in the kidney, and hippuric acid is one of the few substances actually formed by that gland. In the rabbit the synthesis may occur elsewhere, as the animal can form hippuric acid after the removal of the kidneys. The benzoic acid is derived from vegetable food. It is known that hay, grass, and grain contain in their cuticular covering a substance which yields hippuric acid in the body. If the foods be treated with caustic potash, the hippuric-acid-forming substance is removed, and animals fed on this forage form no hippuric acid. Even, it is said, if the husk be removed from grain, the latter is incapable of giving rise to hippuric acid. The benzoic acid derived from the various aromatic bodies contained in plants, is combined with glycine, the latter being derived either from the decomposition of protein substances or from the bile acid. There is a doubt about its source, as no free glycine has been detected either in the blood or tissues. The synthesis occurs in the kidney, and is brought about in the cells of the tubules in conjunction with the oxygen of the red corpuscles, the kidney providing the glycine.

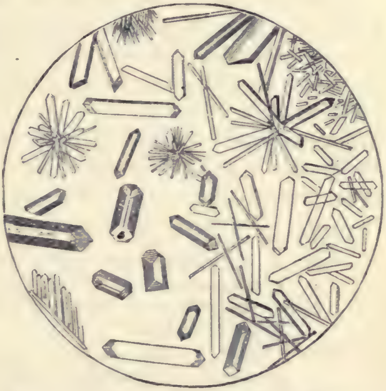

Fig. 99.—Crystals of Purified Hippuric Acid (Funke).

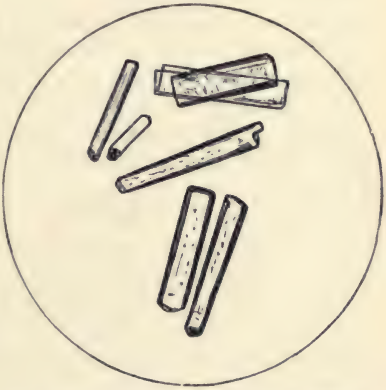

Fig. 100.—Crystals of Impure Hippuric Acid.

Outside the body the synthesis may readily be produced by using ground-up kidney tissue mixed with blood, and kept at the body temperature; but if the kidney be perfused with a mixture of blood, glycine, and benzoic acid, its epithelial cells must be undamaged in order to obtain hippuric acid. This suggests that the active agent in the synthesis is an enzyme.

Another source of hippuric acid is the aromatic (benzoic) products formed in the intestinal canal during the putrefaction of proteins, while it seems clear that a third source is the aromatic residues of tissue proteins, for hippuric acid does not entirely disappear from the urine in starvation. Diet plays an important part in the production of this substance; it is increased by grass, hay, and straw, and decreased by the use of clover, peas, wheat, and oats. The amount of hippuric acid excreted by horses depends, therefore, upon several factors:

On an entirely grass diet a horse will excrete, on an average, 120 grammes daily (4·2 ozs.).
On an entirely hay diet a horse will excrete, on an average, 50 grammes daily.
On a diet of hay, oats, and straw a horse will excrete, on an average, 85 grammes daily.
On a mixed diet the amount may be 60, 140, or 165 grammes daily.

With the usual caution regarding urinary percentages—viz., that they are worthless unless the total amount of secretion is known—it may be said that hippuric acid in the horse exists in the proportion of from $\frac{3}{4}$ to 2 per cent. The amount in cattle and sheep is given on pp. 338, 339.

Liebig, many years ago, stated that benzoic acid was found in the urine of working horses, and hippuric acid in the urine of those at rest. Our observations show that hippuric acid is generally found in the urine of working horses, and seldom found in the urine of horses at rest—in fact, the reverse of Liebig's view. Owing to its easy and rapid fermentative decomposition, hippuric acid is rarely to be found in urine twenty-four hours old; in fifty-four specimens we only found it eight times. This decomposition may be prevented by the addition of a slight excess of milk of lime, and then boiling the freshly voided urine.

Benzoic Acid is the antecedent of hippuric. As just mentioned, it is derived from the benzoic-acid-forming substances in vegetable food; its crystalline form is shown in Fig. 101.

The **Ammonia Salts** present in urine are an index to the neutralisation of acids in the body. Acid substances are produced in carnivora and omnivora, as the result of metabolism, and these would prove highly poisonous were it not that ammonia is simultaneously formed, which neutralises them. This defensive mechanism against acidosis is brought about by less ammonia being converted into urea. When, as occurs in herbivora, there is already an excess of alkali in the diet, a sufficiency of bases is present to neutralise the acid, so that the normal conversion of ammonia into urea continues, and no ammonia appears in the urine. The evidence which bears on this is afforded by the injection of acids into the circulation. This, in a dog, does not alter the reaction of the blood, for ammonia is produced in sufficient quantities to neutralise it. In herbivora, on the other hand, the ready supply of ammonia is not available, the store of vegetable alkaline salts is soon used up, and the animal suffers more acutely, and is more readily killed by acid poisoning than is the case with carnivora. It is rather a difficult matter to increase the acidity of an acid urine. Mineral acids effect it, but if the acid be pushed too far ammonia is split off from the protein in order to counteract toxic results. On the other hand, it is very easy to increase the alkalinity of an alkaline urine. It may be well to explain that the poisoning which occurs from acidosis is due to the reduced carrying power of the blood for carbon dioxide. In consequence, this substance is retained in the tissues with fatal results. The administration of ammonium carbonate by the mouth will not prevent this condition, since it appears in the urine as urea.

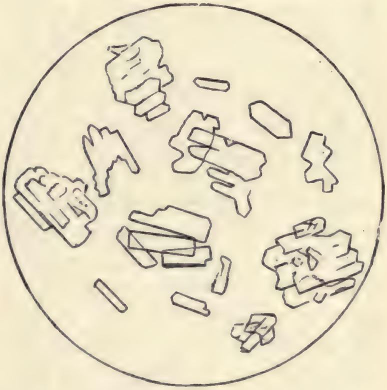
FIG. 101.—CRYSTALS OF BENZOIC ACID.

Free ammonia exists in the urine of the horse. It may be owing to ammoniacal fermentation in the bladder, but it is quite certain that perfectly fresh urine may give marked evidence of the presence of free ammonia. On standing a short time outside the body, especially in summer weather, the urea decomposes, as previously mentioned (p. 322), and ammonium carbonate is largely formed.

Sulphuric Acid.—The sulphates in the urine, especially that of herbivora, and more particularly the horse, are an excretion of considerable importance. In all animals three varieties of sulphur-containing substances are found—viz.:

Inorganic sulphur.
Neutral sulphur.
Ethereal sulphates.

And from this it might be supposed that the sulphates taken into the body with the food represent something considerable. As a matter of fact, the sulphates in food exist only in traces, and the above compounds are really derived from the oxidation of the sulphur of protein substances undergoing disintegration.

The *Inorganic Sulphur* is believed to be derived from the katabolism of proteins in the intestinal canal, or, at any rate, from the destruction of protein substances not yet forming part of the body; hence it is spoken of as the exogenous portion, as in the case of urea and uric acid. The quantity of sulphates excreted in this form varies considerably, as it depends upon the amount of protein in the diet; they pass from the body as salts of sodium and potassium.

The *Neutral Sulphur* is furnished from the actual proteins of the tissues; it is not liable to great variations, and the amount for the individual may even be constant. Included with it is the sulphur of the pigment urochrome and of other minor sulphur compounds, such as ethyl sulphide, found in the urine of the dog, and sulphocyanic acid, said to be a constant constituent of the urine of herbivora.

Coming between the above is a third variety of sulphur compounds—the *Ethereal Sulphates*, which are furnished by the tissue proteins, but also, in part, from non-protein substances. This is a very characteristic group in the urine of the herbivora, especially that of the horse, for they form compounds with such poisonous substances as indol, phenol, skatol, kresol, which are produced in the intestinal canal of the animal, both in consequence of the disintegration of protein substances, the result of bacterial putrefaction, but also from certain benzene constituents in vegetable food. These aromatic and highly poisonous bodies mentioned above are either excreted unabsorbed from the intestinal canal, or if absorbed, unite in the blood-stream with an alkaline sulphate to form conjugated or ethereal sulphates, and in this way are rendered innocuous.

The compounds formed by sulphuric acid with the aromatic bodies are—

Potassium phenyl sulphate.
Potassium kresyl sulphate.
Potassium indoxyl sulphate.
Potassium skatoxyl sulphate.

To the compound potassium indoxyl sulphate the name *indican* has been given. This substance on oxidation yields indigo blue, which is comparatively abundant in the urine of the horse. Phenyl-sulphuric acid in the presence of air undergoes oxidation, and yields *pyrocatechin*, which gives the brown colour to the stale urine of the horse. In the dog glycuronic acid may be united to some of the skatol and phenol, and this substance exercises a reducing action on salts of copper, which might be mistaken for dextrose.

In man and the dog the ethereal sulphates are regarded as a measure of protein disintegration, but in the horse this is not so. Salkowski showed that in the urine of the horse 18·8 grammes of total sulphates were excreted, of which no less than 10·3 grammes belonged to the group of ethereal sulphates.

The *colouring matter of the urine* is a question not fully settled. There are known to be several pigments, the chief one being *urochrome*, which is probably an oxidation product of *urobilin*. Urobilin is formed from stercobilin, which is absorbed from the intestinal canal. The mother-substance of urobilin is a *chromogen*, which yields urobilin on oxidation.

The **Inorganic Substances** found in the urine are calcium, magnesium, sodium, and potassium, existing in the form of chlorides, sulphates, phosphates, and carbonates. The origin of these salts is from the food taken into the body, but mainly from metabolic processes occurring in the tissues. The nature and amount of the salts varies with the class of animal and the character of the food. In the urine of the horse potassium salts predominate, sodium and magnesium are present in small amounts, phosphates are practically absent, while sulphates and chlorides are in considerable quantity. It has been found that in ruminants the calcium salts are mostly excreted with the fæces, whereas in the horse they principally pass through the kidneys. It is certain that phosphates, which form such a prominent feature in the urine of carnivora and omnivora, are in the horse almost wholly excreted by the intestines.

Calcium.—More lime exists in the urine of the horse than is soluble in an alkaline fluid, so that both suspended and dissolved lime exists; the former increases with the age of the urine, owing to the development of ammonia, until nearly the whole of the lime is precipitated. The lime exists in combination with oxalic, carbonic, hippuric, and sulphuric acids; all these combinations do not necessarily exist in one specimen of urine, the salts formed depending on the varying relative amounts of the acids formed in metabolism. The amount of lime in the food does not influence the elimination through the kidneys, but more lime is found in the urine of horses at work than of those at rest. Oxalate and carbonate of lime crystals are common microscopic deposits in the urine of the horse (Figs. 102 and 103). The oxalic acid is derived from the oxalate contained in the vegetable substances of the food.

The turbidity of the healthy urine of the horse is due to suspended lime. This may be proved by the addition of an acid, which causes profuse evolution of gas, and a clear, transparent urine results. Simple as the point is to understand, it would appear in practice that turbid urines in the herbivora are regarded as pathological, and that the marked deposit which follows every evacuation of urine is not compatible with a normal condition. The fact is, that no healthy horse passes anything but a turbid urine, sometimes with a considerable deposit, but always with a deposit. It may be seen in the stall, or better still in the road, after the urine has either soaked in or partly dried, that a fine yellow, sandy-looking deposit exists. The sand is lime; the yellow colour is the pigment of the urine. The remarkable thing is that calculus in the horse is so rare, considering the fact that from the pelvis of the kidney onward the urine has far more mineral matter in it than it can hold in solution.

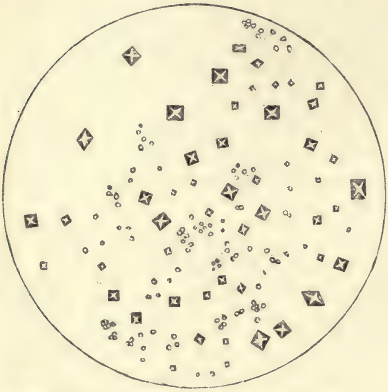

FIG. 102.—CRYSTALS OF OXALATE OF LIME (FUNKE).

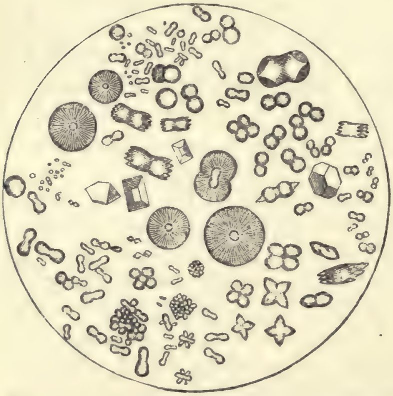

FIG. 103.—CRYSTALS OF CARBONATE OF LIME (FUNKE).

Magnesium in the urine is also suspended and dissolved, the amount which is suspended being increased by the ammonia generated in the urine on standing.

Potassium exists largely in the urine of herbivora, derived from the potash of the food; it forms numerous combinations, the one with carbonic acid being the cause of the fixed alkalinity of the urine in the horse. There is more potash found in the urine of horses at rest than of those at work, which is explained by the considerable amount of potassium excreted with the sweat. **Sodium** only exists in the urine of herbivora in relatively small quantities, which is due to the fact that very little sodium is found in vegetable food.

Chlorine is supplied by the chlorides of the food. The proportion of chlorides in the food of herbivora is not very high; the amount excreted by horses, combined with sodium, was found by us to equal a daily excretion of 5·5 grammes (85¼ grains) of common salt. Salkowski places it much higher—viz., about 27 grammes (¾ ounce) daily.

Phosphoric Acid, though existing largely in food such as oats, passes off almost wholly by the alimentary canal. Sometimes only traces are to be found in the urine of herbivora; at others the amount is marked, but never considerable. Work does not influence its production. In the urine of carnivora the phosphates are an important constituent. They exist in the urine in two forms — viz., alkaline phosphates, such as phosphate of sodium or potassium, and earthy phosphates, such as phosphates of calcium and magnesium; these triple phosphates are common as a microscopical object in the decomposing urine of the horse, though trifling in actual amount (Fig. 104). The phosphates are derived from the food and tissues. According to Munk, if there is an abundance of lime salts in the diet, as in vegetable food, the phosphates are not eliminated to any extent by the kidneys, for the reason that they combine in the intestinal canal with lime and magnesia, and pass off by that channel; if, on the other hand, there is but little lime and magnesia in the intestines, the phosphates are united to soda and potash, pass into the blood, and are eliminated by the urine. In febrile conditions in the herbivora phosphates appear in the urine in marked amounts.

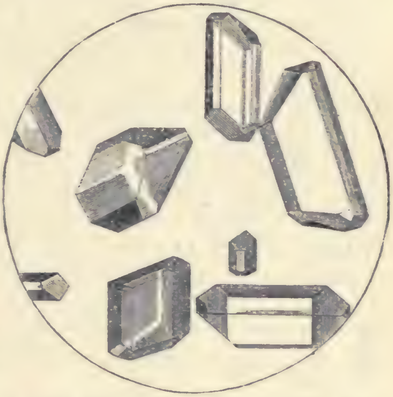

FIG. 104.—CRYSTALS OF TRIPLE PHOSPHATE (FUNKE).

The **Reaction** of the urine of herbivora is alkaline, the alkalinity being due to carbonate of potash. The urine of all vegetable feeders is alkaline, owing to the excess of alkaline salts of organic acids contained in the food, such as malic, citric, tartaric, and succinic. During their passage through the body these salts are oxidised into carbonates, and appear as such in the urine, where they produce considerable effervescence on the addition of an acid. The nature of the food influences the reaction. It is stated that a horse fed on perennial rye grass develops an acid urine, and it is certain that if hay be withheld from the diet, the urine of the horse may be rendered acid by feeding entirely on oats. This is said to be due to hippuric acid in rye-grass feeding. In the case of oats it is probably due to the formation of acid phosphates from the food, due to the absence of vegetable organic acids in the oats.

In the dog the urine is acid, due to the acid phosphate of soda, and not to any free acid; no free acids exist in the urine of any animal. In the pig the reaction is either acid or alkaline, depending on the diet: an animal diet producing an acid and a vegetable diet an alkaline urine. The acidity of the urine may be increased by the use of mineral acids, as we have seen in speaking of ammonia (p. 329). The alkalinity of the urine is increased on standing, especially in summer weather.

The **amount of water secreted** with the urine differs considerably in the various classes of animals. It is generally considered in the horse that of the total intake of water not more than one-third leaves the body by the kidneys. The writer obtained as the mean of many observations, 4·8 litres (8½ pints) of urine in twenty-four hours. This agrees with the observations of Munk,* who regarded 3 to 4 litres as the mean excretion in the horse. In the ox a larger amount of urine is passed—6 or 10 to 25 litres (10, 17, 44 pints) daily. Sheep, 0·3 to 0·9 litre (½ pint to 1½ pints). Pigs, 1·5 to 8 litres (2·6 to 14 pints). Dogs, 0·5 to 1 litre (0·8 pint to 1·6 pints). Tereg,† who gives this table, states that the excretion of water by the kidneys and other channels in the various classes of animals is as follows:

> Herbivora: 20 per cent. excreted by the urine; 80 per cent. by lungs, skin, and bowels.
> Omnivora: 60 per cent. excreted by the urine; 40 per cent. by lungs, kidneys, and bowels.
> Carnivora: 85 per cent. excreted by the urine; 15 per cent. by lungs, skin, and bowels.

Food rich in nitrogen causes a greater secretion of urine.

Urine of the Horse.

Specific Gravity.—This varies within wide limits dependently on the diet and the amount of dilution. The mean of a large number of observations was 1036, the highest registered was 1050 and the lowest 1014.

The *Quantity* of urine is liable to very considerable variation, depending on the season and the diet; the more nitrogen the food contains the larger the amount of water consumed, and the greater the bulk of urine excreted. The mean of a large number of observations was 4·8 litres (8½ pints) in twenty-four hours, the diet being moderately nitrogenous, but in individual instances very much more than this may be met with—viz., 6 to 11 litres (12, 15, or even 20 pints).

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* Quoted by McKendrick.

† Ellenberger, *op. cit.*

Horses at work excrete less urine than those at rest, no doubt owing to the loss by the skin. In winter, in consequence of the lessened action of the skin, more urine is excreted than during summer.

The *Odour* of urine is said to be due to certain aromatic substances of the phenol group. Perfectly fresh urine has commonly a most distinct though faint smell of ammonia. This may be due to fermentative changes occurring in the urea before the urine is evacuated. The normal fluid is always turbid, some specimens more so than others ; very rarely is it clear, and then only for a short time. The turbidity is due to the amount of suspended carbonate of lime and magnesia it contains ; as the urine cools, particularly if it undergoes ammoniacal fermentation, the amount of turbidity becomes intense (see p. 331).

The *Consistence* of the fluid depends upon sex, and perhaps on the season. It is certain that some mares excrete a glairy, tenacious fluid which, owing to the amount of mucin it contains, can be drawn out in strings ; it is very common to find it as thick as linseed oil, and very rare to find it fluid and watery. During œstrum the urine is of the consistence of oil. On a diet of oats and no hay, the urine may be so mucinous as to pour like white of egg.

The *Colour* of urine is yellow or yellowish-red, rapidly turning to brown, the dark tint commencing on the surface of the fluid, and gradually travelling into its depth. The cause of the colour on standing is due to the oxidation of pyrocatechin (see p. 330).

The *Total Solids* consist of organic and inorganic matter, of which, on a mixed diet, 142 grammes (5 ounces) are organic, and 85 grammes (3 ounces) inorganic ; the quantities are liable to great variation, sometimes being found greatly in excess of that mentioned. The total solids are considerably affected by the diet ; E. Wolff* found that when he reduced the hay and increased the corn ration, the solids in the urine decreased, whereas on a diet consisting principally of hay and but little corn the solids increased ; for example—

> On a diet of 8 kilogrammes of hay and 2 kilogrammes of oats there were 566 grammes of total solids.
>
> On a diet of 4 kilogrammes of hay and 6 kilogrammes of oats there were 460 grammes of total solids.

The composition of the mineral solids is given in the following table by Wolff, the diet being hay, oats, and straw. In every 100 parts of salts there are found—

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* Ellenberger.

Potassium	36·85 per cent.
Sodium	3·71 ,,
Calcium	21·92 ,,
Magnesium	4·41 ,,
Phosphoric acid	—
Sulphuric acid	17·16 ,,
Chlorine	15·36 ,,
Silicic acid	0·32 ,,

In the table on p. 337 are given the results obtained by the writer in the examination of the twenty-four hours' urine of horses at rest and work.*

Salkowski† examined the urine of the horse, and gives the following as the composition of one specimen:

Water	1·8 litres	3·50 pints
Organic solids	198·0 grammes	6·25 ounces
Ash	50·0 ,,	1·60 ,,
Urea	92·0 ,,	3·25 ,,
Ammonia	0·357 gramme	5·53 grains
Hippuric acid	15·60 grammes	0·49 ounce
Phenol	2·44 ,,	37·89 grains
Organic sulphur	13·46 ,,	208·69 ,,
Inorganic sulphur	5·33 ,,	85·77 ,,
Phosphoric acid	0·22 ,,	3·40 ,,
Lime	5·70 ,,	88·50 ,,
Sodium chloride	27·12 ,,	0·87 ounce

In the following summary of the urine of animals other than the horse, the main facts are those given by Tereg.‡

The Urine of the Ox.

The urine of the ox is much the same as that of the horse, excepting that it is secreted in larger quantities, 5·7 to 22·8 litres (10 to 40 pints); the difference mainly depends upon the amount of nitrogenous matter in the diet, for it has been shown that the more nitrogen a diet contains the larger the amount of water consumed. The fluid is clear, yellowish, and of an aromatic odour; it is of a lower specific gravity than that of the horse, 1020 to 1030 (in milch cows, according to Munk, 1006 to 1015), owing to the larger amount of water secreted. The nitrogenous matter found in the urine is mainly represented by urea and hippuric acid, and the amount varies according to the diet. On a diet of wheat straw, clover hay, beans, starch, and oil, the

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* 'Chemistry of the Urine of the Horse,' Proceedings of the Royal Society, vol. xlvi., 1889.

† Ellenberger's 'Physiologie.'

‡ *Ibid.*

	Rest.		Work.	
Quantity	5·0 litres	8·69 pints	4·5 litres	7·88 pints
Specific gravity	—	1036	—	1036
Total solids	230·0 grammes	8·11 ounces	232·0 grammes	8·19 ounces
Organic solids	146·0 ,,	5·15 ,,	152·0 ,,	5·37 ,,
Inorganic solids	83·0 ,,	2·94 ,,	80·0 ,,	2·82 ,,
Urea	98·4 ,,	3·47 ,,	98·4 ,,	3·47 ounces
Ammonium carbonate as urea	13·0 ,,	0·46 ounce	13·0 ,,	0·46 ounce
Ammonia	2·5 ,,	0·09 ,,	5·4 grammes	0·19 ,,
Benzoic acid	6·5 ,,	0·23 ,,	—	—
Hippuric acid	—	—	15·6 grammes	0·55 ,,
Phosphoric anhydride	1·13 grammes	0·04 ,,	1·7 ,,	0·06 ,,
Sulphuric anhydride	10·5 ,,	0·37 ,,	15·3 ,,	0·54 ,,
Other sulphur compounds	7·37 ,,	0·26 ,,	7·6 ,,	0·27 ,,
Chlorine	31·7 ,,	1·12 ounces	21·8 ,,	0·77 ,,
Calcium oxide	3·4 ,,	0·12 ounce	1·7 ,,	0·06 ,,
Magnesium oxide	2·8 ,,	0·10 ,,	2·5 ,,	0·09 ,,
Potassium oxide	33·7 ,,	1·29 ounces	27·0 ,,	0·95 ,,
Sodium oxide	2·5 ,,	0·09 ounce	1·7 ,,	0·06 ,,

amount of urea may be 4 per cent., while on one of oat straw and beans, it may fall to less than 1 per cent. When the urea is high, the hippuric acid is low, and *vice versa.* The largest amount of hippuric acid is produced by feeding on the straw of cereals, the smallest is furnished by feeding on leguminous straw, whilst a medium amount is produced by feeding on hay. It was stated many years ago by Faas that the urine of the working ox is turbid, and contains so much hippuric acid that a pound of this substance could be obtained by precipitation with hydrochloric acid. The amount of urine from which it was extracted is not given. The urine of ruminants contains less aromatic sulphur compounds than that of the horse, and more of the inorganic sulphur; like the horse, the phosphates are either absent or only occur in small amounts.

The following table by Tereg shows the composition of the urine of the ox on different diets; the observations extended over four months:

	Kilos.	Lbs.	Kilos.	Lbs.	Kilos.	Lbs.	Kilos.	Lbs.
Total urine	11·83	26·02	14·17	31·17	13·63	29·98	8·33	18·32
Dry matter -	0·78	1·71	0·69	1·51	0·64	1·40	0·52	1·14
Ash - -	0·40	0·88	0·46	1·01	0·47	1·03	0·30	0·66

On a diet of 8·45 kilogrammes of meadow hay, the urine gave the following composition:

Quantity - - - -	7·57	kilogrammes.
Specific gravity - - -	1042	
Hippuric acid - - -	98·0	grammes.
Urea - - - - -	131·0	,,

Calves still suckling excrete an acid urine which is rich in phosphates, uric acid, kreatinine, and a peculiar substance known as allantoin. It is poor in urea, and, according to Moeller, contains hardly 1 per cent. of solids.

The Urine of the Sheep.

This has an alkaline reaction, a specific gravity of 1006 to 1015, and the amount excreted varies from 0·3 to 0·9 litre (0·5 pint to 1·5 pints). Tereg gives the following percentage composition of a sample:

Water - - - - - -	86·48
Organic matter - - - -	7·96
Inorganic matter - - -	5·56

The organic matter contained—

Urea	2·21
Hippuric acid	3·24
Ammonia	0·02
Other organic substances	2·07
Carbonic acid	0·42
	7·96

The inorganic matter contained—

Chlorine	1·05
Potassium chloride	1·84
Potassium	2·08
Lime	0·07
Magnesia	0·20
Phosphoric acid	0·01
Sulphuric acid	0·24
Silica	0·07
	5·56

In sheep urea and hippuric acid stand in the proportion of 2 to 3, whereas in cattle on the same diet the proportion is 2 of urea to 1·1 of hippuric acid. The food most productive of hippuric acid in the horse is old meadow hay, whilst *new* meadow hay has this effect on sheep. It will be observed from the table how rich the urine of the sheep is in hippuric acid. In sheep there is very much more magnesia than lime in the urine, consequently the reverse obtains in the fæces of this animal.

The Urine of the Pig.

This resembles that of carnivora, but its composition depends on the character of the food. The specific gravity is 1003 to 1025. It is either acid or alkaline ; the amount excreted varies between 1·5 to 8 litres (2½ to 14 pints), and it contains uric acid, hippuric acid, xanthine, guanine, and much urea.

In the following analysis of the urine the diet consisted of peas, potatoes, and sour milk :

Total urine	4·1 kilogrammes (7 pints).
Specific gravity	1018
Dry substance	2·768 per cent.
Total nitrogen	0·604 ,,
Ammonia	0·024 ,,
Ash	1·234 ,,

The ash consists largely of phosphates and potassium salts, a moderate amount of magnesium, and very little sodium or calcium.

The Urine of the Dog.

It is impossible to give the composition of the urine of the dog, as the amount of constituents secreted varies considerably in dependence upon the nature of the diet.

The urine is acid in reaction on a flesh diet, the acidity being due to acid phosphate of soda ; on a vegetable diet it may be alkaline. The amount excreted is from 0·5 to 1 litre (¾ pint to 1¾ pints) daily, but varies with the size of the animal and the nature of the diet; the specific gravity is from 1016 to 1060, depending on the diet; the colour is pale yellow to straw-yellow; the urea varies from 4 per cent. to 6 or 10 per cent. On an animal diet uric acid is excreted, but disappears on giving vegetable food; hippuric acid in small quantities appears with fair regularity; indican and phosphoric acid are well-marked constituents, and a substance known as glycuronic acid may be found, which exercises a reducing action on salts of copper. The presence of bilirubin in the urine of the dog has been noted by Salkowski.

As an illustration of the variation of the dog's urine dependently on the nature of the diet, we may take an example from a long series of experiments by Bischoff and Voit.

On a diet consisting of meat 0·57 pound, starch 0·71 pound, salts 77·5 grains, a specimen of urine gave the following composition:

Amount - - - -	252 c.c.	0·44 pint.
Specific gravity - -	—	1049
Urea - - - -	21·0 grammes	326·6 grains
Salts - - - -	5·53 ,,	85·6 ,,

On a diet consisting of meat 2·75 pounds and fat 0·55 pound, the following was the composition:

Amount - - - -	702 c.c.	1·23 pints
Specific gravity - -	—	1054
Urea - - - -	80·7 grammes	1,351 grains
Salts - - - -	12·21 ,,	189 ,,

Glycuronic acid exists only in traces, but after the administration of camphor or chloral it is obtained in well-marked quantities. It is a point of practical importance to avoid regarding urine which reduces salts of copper as necessarily containing sugar, for glycuronic acid is itself reducing.

The Discharge of Urine.—The urine is constantly being secreted, and it either trickles down or is propelled down the ureters to the bladder by rhythmic muscular contractions. It is quite likely that both movements are employed, depending upon the condition of bladder distension; whereas 'trickling' is suitable for an empty bladder, some muscular effort on the part of the ureters would be required when the bladder is full. Either drop by drop or by 'spirts' the urine enters the bladder, which gradually advances in the pelvis, and rises up in the direction of the sacrum. All reflux of urine into the ureters is prevented by the oblique manner in which the coats of the bladder are pierced, so that the greater the internal strain the tighter are the ureters closed. If circumstances prevent the evacuation of the bladder contents, the organ gradually advances to the brim of the pelvis, and then impinges on the abdominal cavity ; in a state of extreme distension it may project for some distance into the cavity, the weight of the fluid having a tendency to cause the organ to incline towards the floor of the abdomen

The entrance to the urethra is controlled by a circular layer of unstriped muscle, part of the bladder muscle, but outside this is a band of voluntary muscle, which must be regarded as part of the urethra. Physiologists are not agreed as to the mechanism involved in the act of micturition. Ordinarily it is a voluntary act, but the dog with its spinal cord divided in the lumbar region, will carry out the process perfectly, though there can be no question of consciousness involved. In this case the afferent impulses conducted to the cord by the second and third sacral nerves stimulate a *vesical centre*—the grey matter of the sacral cord. There can be no doubt that, under ordinary circumstances, the act is a voluntary one. The efferent nerves supplying the bladder are derived from two sources—viz., directly from the sacral spinal nerves, and a second supply through the sympathetic. The sacral nerves furnish the *nervus erigens*, which is connected with the hypogastric plexus, while the sympathetic supply is furnished by the second to the sixth lumbar ganglia ; these pass to the inferior mesenteric ganglion, and issue from it as the hypogastric nerves. Stimulation of the *nervus erigens* causes relaxation of the sphincter and contraction of the wall of the bladder, while the hypogastric nerves, though relaxing the wall of the bladder, contract the sphincter. In the latter action it is antagonistic to the spinal nerve supply. It is almost certain that the most important source of supply to the bladder is that furnished by the *nervus erigens*.

At the moment the bladder wall begins to contract, it is assisted by the abdominal muscles and a fixed diaphragm, and the flow is never as powerful in the female as in the male, the final expulsion of the last drops from the urethra of the latter being given by the rhythmical contraction of the perineal muscles and *accelerator urinæ*. During the act both the horse and mare stand with the hind-legs extended and apart, resting on the toes of both hind feet, thereby sinking the posterior part of the body ; the male animal also often advances the fore-legs in order to avoid getting them splashed ; in this position the penis is protruded, and the tail raised and quivering. The stream which flows from the two sexes is very different in size, depending on the relative diameters of the urethral canal. The mare after urinating spasmodically erects the clitoris, the use of which it is difficult to see ; it may be due to the passage of a hot alkaline fluid over a remarkably sensitive surface. The horse can, under ordinary circumstances, only pass urine when standing still, though both sexes can defæcate while trotting; but in a condition of œstrum the mare can empty her bladder while cantering. In the ox the urine simply dribbles away, owing to the curves in the urethral canal, and is directed towards the ground by the tuft of hair found on the extremity of the sheath. The ox can pass his urine while walking. The cow arches her back to urinate, but instead of extending her hind-limbs, as does the mare, she brings them under the body, at the same time raising her tail.

The upright position is essential to micturition; no horse of either sex can evacuate the bladder while lying down—a point of extreme importance in practice. Further, it will be remembered that in an over-distended bladder the fundus hangs into the abdominal cavity, and is thus brought on a lower level than the urethra, both of which contribute to the difficulty of emptying an over-distended organ. As a horse cannot micturate at work, it is obvious that opportunity for this should be regularly afforded, or much suffering results.

Pathological.

There is scarcely any organ of the horse's body so free from disease as the kidneys. The material in the pelvis which looks like pus is really the natural mucus of the urine, mixed with insoluble lime salts. We have never found sugar in the horse's urine; protein is not uncommon, but only as the result of inflammatory affection of the lungs and pleura.

Vesical calculus would be one of the most common diseases among the herbivora, but for the fact that they excrete the insoluble salts at each evacuation, and calcium carbonate has but little tendency to cohere.

CHAPTER XI

NUTRITION

Wear and tear is continually taking place in the bodies of all animals, and as fast as destruction occurs repair must follow. We have previously studied the various channels in the body which supply the income and furnish an outlet for the expenditure, but this is only the beginning and the end of the process. To attempt to trace the exact changes which occur, say in the body of a pig, in producing 1 pound of living material from 5 pounds of barley-meal, is an impossibility. All we can do is to interpret the coarser or more obvious processes which take place, that of the conversion of dead into living tissues being quite beyond our knowledge.

Composition of the Body.—The animal body consists of proteins, fats, salts, water, and a very small proportion of carbohydrate. Every food must either contain these principles, or be capable of conversion into them within the animal body. The following table from Lawes and Gilbert* shows the relative proportion of these various tissues in oxen, sheep, and pigs, in lean and fat condition:†

	Oxen.		Sheep.		Pigs.	
	Lean.	Fat.	Lean.	Fat.	Lean.	Fat.
Water - - -	60·8	51·0	63·5	51·5	61·2	43·7
Nitrogenous substances - -	18·0	15·0	15·0	12·5	14·0	10·5
Non-nitrogenous substances (fat)	16·0	30·0	18·0	33·0	22·0	44·0
Mineral matter -	5·2	4·0	3·5	3·0	2·8	1·8
	100·0	100·0	100·0	100·0	100·0	100·0

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* 'Chemistry of the Feeding of Animals,' a lecture before the Royal Dublin Society, 1864, by John Bennett Lawes, F.R.S.

† It is assumed that the stage of fatness is a maximum when the ox or sheep has increased in weight by about half, and the pig has doubled its weight.

The water is always in the largest and, excluding the carbohydrate, the salts in the smallest proportion. The proportion of protein and fat in the body depends upon the condition of the animal; the proportion the protein bears to the fat depends not only on the condition, but on the class of animal. The lean ox for a given weight has more nitrogenous substances than fat; but in the sheep and pig this is reversed. In the fat animal there is always more fat than nitrogenous matters. There are more water and salts in the lean than in the fat animal; while the ox has more mineral matter than the sheep, and the sheep more than the pig.

The following table shows the proportion of the chief body tissues of an adult horse weighing 1,100 pounds, and it may be compared with that of a cat:

	Horse.	Cat.
	Per Cent.	Per Cent.
Muscles and tendons	45·00	45·0
Bones	12·40	14·7
Skin	6·02	12·0
Blood	5·90	6·0
Abdominal viscera	5·49	—
Thoracic viscera	1·60	—

According to Lawes and Gilbert, the following are the relations of these parts in the ox, sheep, and pig for every 100 pounds of living weight:

	Ox.	Sheep.	Pig.
Heart, lungs, liver, blood, and spleen	7·0	7·3	6·6
Internal loose fat	4·6	6·9	1·6
Stomach and contents	11·6	7·5	1·3
Intestines and contents	2·7	3·6	6·2
Other offal parts	13·0	15·0	1·0
Muscle, bone, and surrounding fat	59·3	59·2	82·6

The bulk of the body is seen to be represented by the muscles, and these hold half the water and half the protein found in the system.

Income and Expenditure.—The *Income* of the body consists of carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, salts, and water. These are contained in the food, the oxygen being mainly supplied by the air taken in at the lungs.

The *Expenditure* consists of the same elements, which are got rid of by the lungs, urine, fæces, and skin.

The **nitrogen** is excreted almost wholly by the urine, excepting in the horse, where there is a loss by the skin. It is usual to regard the urine-nitrogen as a measure of the protein changes in the system, and this passes away mainly as urea, and in smaller proportion as uric and hippuric acids and other nitrogen compounds. The **hydrogen** is excreted as water by the lungs, skin, and urine, and in all herbivora by the bowels and respiratory passages as marsh-gas.

In order to arrive at the processes involved in nutrition, tables of income and expenditure of the body for twenty-four hours have been drawn up. For this purpose a **Respiration Chamber** is employed, in which the animal under observation lives. The air supply to the chamber is dried and freed from carbon dioxide. Ventilation is carried out by means of a pump, and from time to time samples of the air are analysed, in order to determine the amount of O_2 absorbed and CO_2 given off. The composition of the food is known, and the total excreta analysed, in order to ascertain to what extent this differs from the food entering the body. In this way the chemical elements entering the body as food and leaving it as excreta are known. When these are found to be practically identical, the animal is in metabolic balance. There is probably no class of experiment so tedious as this. The work is continuous for twenty-four or forty-eight hours, and a very small error in the technique renders the whole observation useless. In the latest form of respiration chamber for men means have been introduced to enable a definite amount of work to be performed, and in this way the metabolism of the body at work as well as at rest can be ascertained. The most advanced method of inquiry is the **Respiration Calorimeter**, in which not only the nitrogen and carbon balance can be ascertained, but also the heat given out by the body. By means of the respiration calorimeter not only is the proportion of the digestible matter in the food ascertained, but also the potential energy contained in it, and the use the body makes of the material supplied. Recently such an appliance for large animals has been erected at the Institute of Animal Nutrition of the Pennsylvania State College.* It is extremely costly, and so elaborate that it takes seven men to work it, exclusive of those in attendance on the animal. The ordinary calorimeter employed in physiological research is figured in the chapter on Animal Heat. It is a double-walled chamber containing water. As the temperature of the chamber rises, the heat is conveyed to the water in its walls, and its temperature measured. The respiration calorimeter used for animals is copied from the one employed by Atwater in his classical experiments on nutrition in men.

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* See Bureau of Animal Industry, Twenty-Third Report, p. 263.

The animal is enclosed within three sealed walls, each separated by an air space, the inner one being the calorimeter. Food for the period is supplied by a specially arranged door, the excreta collected, and the heat of the chambers registered. The heat is absorbed by a current of cold water passing through copper pipes at the top of the respiration chamber; . . . the temperature of the ingoing and outcoming water is read every four minutes by means of two thermometers graduated to $\frac{1}{50}$° C. The inner wall of the chamber is copper and zinc, with a 3-inch dead space between each metal; these are connected by 600 couples connected in series, with a reflecting galvanometer, serving to indicate any difference in temperature between the inner and outer surface. Special arrangements exist for heating or cooling this air space so as to rectify any difference which may exist. The temperature of the chamber is registered by means of a series of copper resistance thermometers, connected to a slide wire Wheatstone bridge. All the heat evolved by the animal must leave the apparatus either as sensible heat in the water current, or as latent heat of water vapour. So delicate is the apparatus that corrections have to be made for the heat arising from the friction of water in the coil of copper pipes.

The respiratory portion of the apparatus is furnished with a special form of pump which can be graduated to deliver a given number of litres of air per minute; the same pump is regulated to deliver a given quantity of air at special intervals for analysis. Another pump draws this air through the special apparatus, which determines the water and CO_2, after which it passes through appliances where the combustible gases are determined. The plan of this apparatus is seen in Fig. 105, while the general arrangements outside the chamber for its efficient working are seen in Fig. 106.

The following example of a balance experiment—viz., the amount of nitrogen and carbon received and got rid of—was performed with the above apparatus. The animal was a steer. The rations consisted of 4,531 grammes (9·9 pounds) hay and 400 grammes (0·88 pound) linseed-meal.

	Nitrogen.		Carbon.	
	Income.	Outgo.	Income.	Outgo.
	Grammes	Grammes.	Grammes.	Grammes.
The hay contained -	23·4	—	1337·6	—
The linseed-meal contained - - -	22·2	—	172·5	—
The fæces contained -	—	16·2	—	649·8
The urine contained -	—	36·3	—	88·1
The hair, etc., contained	—	1·3	—	8·0
The carbon dioxide contained - - -	—	—	—	934·1
The methane contained	—	—	—	55·2
Lost by body - -	8·2	—	225·1	—
	53·8	53·8	1735·2	1735·2

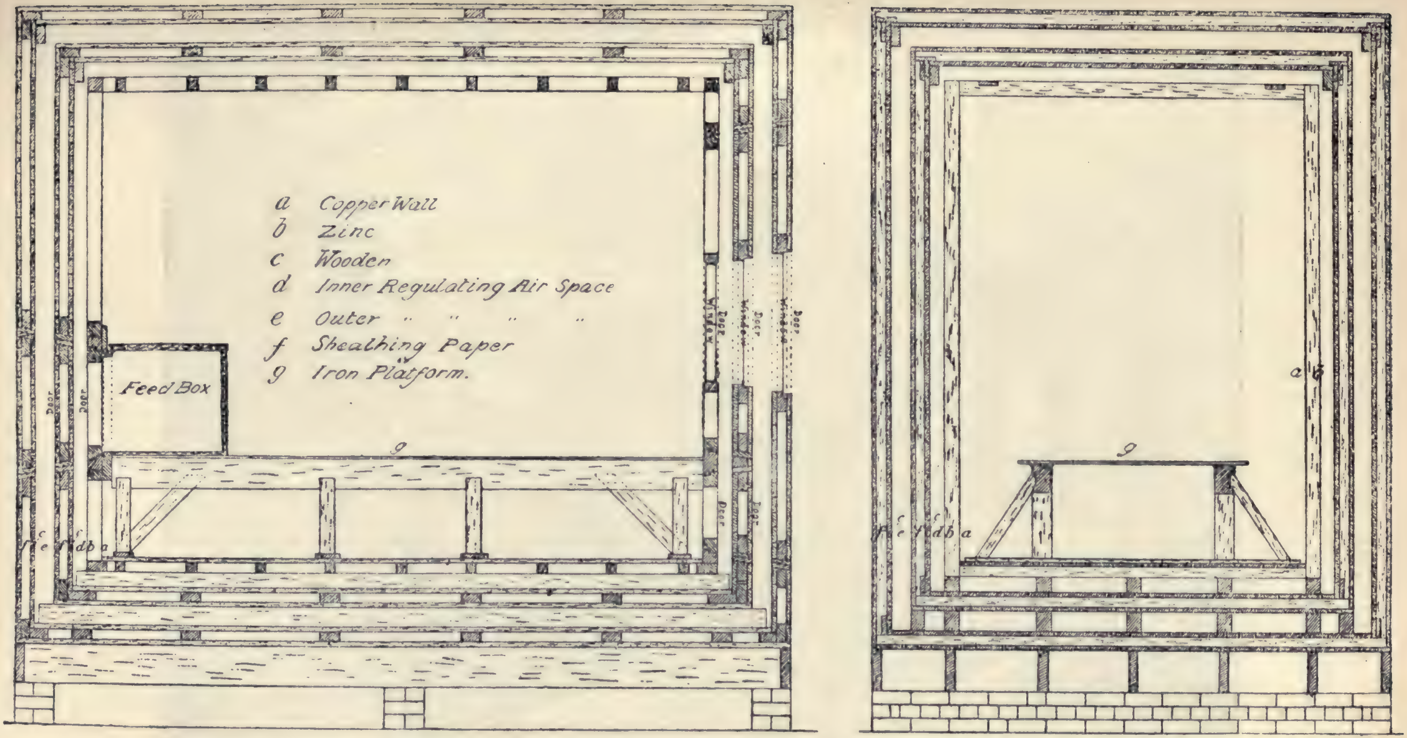
a Copper Wall
b Zinc
c Wooden
d Inner Regulating Air Space
e Outer " " "
f Sheathing Paper
g Iron Platform.
Feed Box
Door
Window
g
f c e f d b a
a b

FIG. 105.—THE ATWATER-ROSA RESPIRATION CALORIMETER FOR ANIMALS: VERTICAL CROSS SECTIONS.

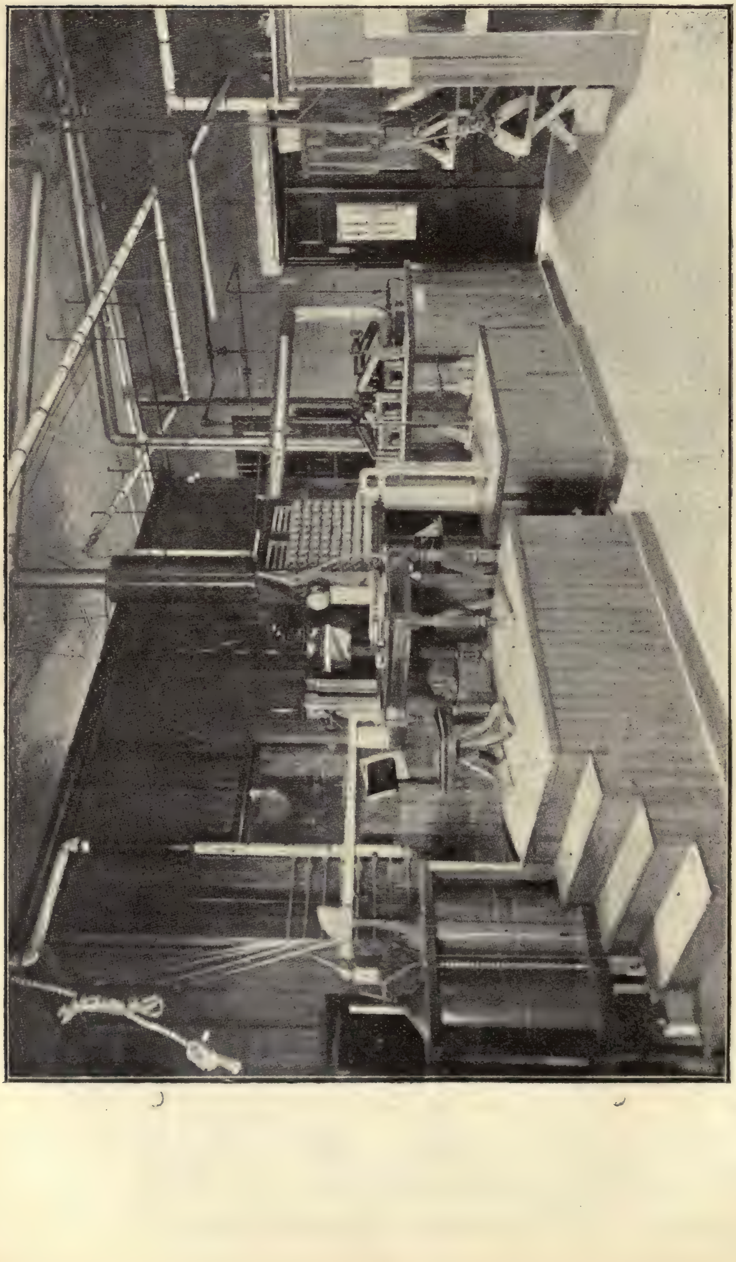

FIG. 106.—THE PENNSYLVANIA RESPIRATORY CALORIMETER FOR ANIMALS ARRANGED FOR EXPERIMENT. The chamber is on the other side of the glass window, to the left of the observer's chair.

In this case the animal lost 8·2 grammes nitrogen and 225·1 grammes of carbon more than it received in the food.

8·2 grammes nitrogen = 49·2 grammes protein.
225·1 grammes carbon = 259·0 grammes fat.

In this example of the balance of matter it is evident the diet was insufficient, and the extent to which this was so, both in nitrogenous and non-nitrogenous substances, is revealed. Up to this point the use of the calorimeter is not very evident, nor can we in this place conveniently discuss the point, as it is concerned, not with the balance of matter, such as is determined above, but with the *balance of energy*, which will be considered presently.

When the income of the body in food balances the expenditure, the body is in equilibrium ; if the income is in excess of the expenditure, the body gains weight ; if the expenditure exceeds the income, as in the above example, the body loses weight.

Metabolism.—By this term is understood the changes occurring in living tissues. It is evident, from what has been said, that constant breaking down and building up is taking place in the body. Every muscular contraction, every respiration, the beating of the heart, and the movements of the bowels, all mean wear and tear, and as rapidly as a part is destroyed it must be replaced. The process of construction is known as **anabolism**, and of destruction as **katabolism.** In a perfect state of health these should be in equilibrium. Both repair and destruction are dependent upon definite chemical changes occurring in the system, of some of which we have a fair knowledge, while others are wrapped in obscurity.

The metabolism of the tissues is apparently under the influence of the nervous system. We have previously studied a good example of this in dealing with the secretory nerves of the submaxillary gland, and it is probable, though our information on the point is very defective, that the nutrition of the body is largely maintained under the guiding influence of the nervous system. We constantly observe muscular wasting in some forms of lameness and injury in the horse, which is out of all proportion to the atrophy a part suffers by being simply thrown out of use, and it can only be explained by injury to the trophic nerves which regulate the nutrition of the part. Even a better example is the peculiar changes which sometimes follow direct injury to trophic nerves, as in plantar neurectomy of the horse. The sloughing of the entire foot, or gelatinous degeneration of the phalanx, is due to injury of the trophic nerves. Injuries to the fifth pair of nerves have been followed by sloughing of the cornea, and pneumonia has followed division of the vagi, in both cases being possibly due to the loss of trophic influence, though much may be said in support of the view that the effects observed may be due to failure of the mechanically protective arrangements of the parts affected, the failure resulting from section of the merely motor and sensory fibres which the respective nerves contain.

But disordered nutrition of a tissue may show itself without any obvious injury to trophic nerves—as, for example, in the phenomenon known as inflammation, or the well-known sympathy existing between the digestive system of the horse and the laminæ of the feet. Further evidence of nervous action is afforded in nutrition which is normal in character, such as the change of the coat with the season of the year. The influence of light on metabolism is also probably effected through the nervous system. It is generally considered that a connection between visual sensations and the nutrition of the skin exists in blind men and animals, and the popular belief that a blind horse carries a heavy coat in summer and a short one in winter may be something more than mere superstition. In making these statements we must guard against the error of considering that no growth, repair, or reproduction can take place excepting under the influence of the nervous system. The trophic influence exercised by nerves appears to be directed to maintaining in equilibrium the processes of building up and breaking down which are occurring in all tissues. Though the metabolism of the body is largely regulated by the nervous system, yet the process cannot be carried out without food. It is true that metabolism goes on during starvation, but even then food is being supplied, inasmuch as the animal is living on its own tissues.

The food must contain the elements required by the tissues—viz., water, protein, fat (or carbohydrate), and salts. Each of these must be in proper proportion, neither deficient nor in excess of the animal's requirements ; each must be present, fat cannot be substituted for proteid, nothing can take the place of salts, and a water-free diet sustains life less long than does the entire absence of food as long as water is consumed. We have, therefore, to inquire why it is these substances are absolutely essential in every diet, and how they behave in the system.

Nitrogenous Equilibrium.—The storing up of protein is an expression which has repeatedly occurred during the previous chapters, and a natural impression may have been created that of the total protein in a diet some of it is daily stored up, so that less leaves the body than entered it by the mouth. There can be no doubt that some of the daily protein of the diet is stored up, but the greater part is not. There can be no more familiar fact than that the body may continue from month to month at much the same weight, and that could never be the case if storing up occurred daily. What occurs is this, that of the total amount of nitrogen received daily in the food, a similar amount is recovered daily from the urine. Whatever portion of the protein of the food is converted into tissue protein, an equivalent amount of the latter is displaced, so that the total excretion of nitrogen equals the total receipts. A body in this condition is in nitrogenous equilibrium. It does not follow from this that it is not increasing in weight; it may be, owing to excess of non-nitrogenous food; on the contrary, it may be losing weight, due to a deficiency of non-nitrogenous material. The matter is of no moment at present, the main point being that in the urine an equivalent amount of nitrogen is excreted to that received in the food, and such an animal is in nitrogenous equilibrium. It is obvious that nitrogenous equilibrium cannot exist in young growing animals, nor in those in impoverished condition. In both these cases nitrogen is being stored up, as the tissue requirements are considerable, so that under these circumstances any attempt to establish nitrogenous equilibrium experimentally would fail. An adult animal in good condition gives off daily by the excreta as much nitrogen as it receives in the diet. If the ingoing nitrogen is increased, the outcoming nitrogen is increased; if the ingoing nitrogen is decreased, the outcoming nitrogen is decreased, and this is true within physiological limits.

It is evident, therefore, that in the same animal there may be different levels of nitrogenous equilibrium, and these are dependent entirely on the income. The more the body receives, the more it spends; the less it receives, the less it gets rid of, the predominant feature being that the system is determined to make its expenditure of nitrogen equal its income. This being the case, how does the body behave when it receives no nitrogen? The improvident expenditure of nitrogen previously existing is now rectified. None is being received by the mouth, and the store in the tissues is therefore most economically handled. On the second day of starvation, by which time the nitrogen of the last meal is eliminated, the output of nitrogen falls suddenly, and after that it remains either at a constant minimum or sinks gradually until death approaches, when, after a temporary rise in the amount excreted, it rapidly falls. It must not be imagined that in this experiment the animal is living exclusively on its own protein. Its body fat is also being utilised, and so long as this lasts a steady daily loss of nitrogen occurs; but when the fat has disappeared, there is an increase in nitrogen excretion, as shown by the temporary rise above noted. The fact is that so long as the fat lasts, the waste of protein is kept down to the lowest possible limit, the fat being sacrificed to spare the protein.

The sacrifice having been effected, the last remaining body substance, the proteins, has then to bear the full brunt of the system's necessities. A starving animal may therefore be kept alive a longer time by receiving some carbohydrate and fat. It will die because it is not receiving nitrogen, but the mixed carbohydrate and fat will effect economies in the store of body protein, and cause it to last longer. In this respect the carbohydrate is of much more value than the fat.

It was reasonable to suppose, as Liebig did, that the protein substances of the food carried out the mechanical work of the body. We now know better, for we have learned from the facts connected with nitrogenous equilibrium that the body continues to work satisfactorily though the equilibrium is established at different levels. Nevertheless, nitrogenous equilibrium, which we have seen possesses characteristic peculiarities, is effected by excessive work in man and severe work in the dog, though within normal limits it is correct to say it is unaffected by work.

The views laid down by Liebig were never seriously disputed until Lawes and Gilbert had completed their twenty years' classical work on animal nutrition at Rothamstead. During the years 1849-1859 these observers gave their results to the world, and their accuracy has never been challenged. Though working at the question of the fattening of animals, and not the question of energy, they were the first to announce that the value of food for feeding purposes could not be based on the so-called flesh-forming substances it contained, but on the non-nitrogenous elements. It is usual in physiology to attribute the demolition of the Liebig theory to the celebrated ascent of the Faulhorn by Fick and Wislicenus in 1866. We shall see presently the manner in which Lawes and Gilbert arrived at their results.

We can now understand why it is that nitrogenous equilibrium experimentally produced is accomplished on a smaller amount of protein when non-protein substances enter into the diet. No animal, not even the carnivora, lives entirely on protein. The effect of the non-protein portion is to reduce the amount of protein destroyed, and establish equilibrium at a lower level. Fat, starch, and sugar are protein economisers, while, conversely, a large protein diet is a fat obliterator, and this fact was turned to account by Banting in his treatment of obesity.

If a fasting animal be brought on to a protein diet equivalent to the amount of nitrogen being daily excreted, it would be reasonable to suppose that nitrogenous equilibrium would at once be established. Experimental inquiry shows this is not so, but that the effect of giving nitrogen is to cause a greater excretion of this substance. It is not, in fact, until an amount of protein is given equivalent to two and a half times the daily excretion during fasting that equilibrium is established. Protein only contains from 50 to 54 per cent. carbon, and the reason why the animal under the above conditions goes on consuming more and more protein until the balance is restored, is to enable the required amount of carbon to be obtained. This fact explains the extravagant nature of protein diets. It enables us to understand the loss in body weight which may be occurring even when nitrogenous equilibrium is established, and to grasp the fundamental principle in feeding—that carbohydrate or fat, containing 76·5 per cent. carbon, enables equilibrium to be established on a lower plane in consequence of the economical effect they exert on protein. In the case of a dog in nitrogenous equilibrium, less than two-thirds the amount of protein will suffice to produce this result if a small amount of fat or carbohydrate form part of the diet. The economising effect of fat, starch, and sugar on protein is one of the few well-established facts in dietetics.

The History of Protein in the Body.—When describing the digestion of protein substances in the digestive canal, sufficient was said to indicate the big gaps which exist in our knowledge of this question. Still greater ignorance exists of the subject now to be considered—viz., the behaviour and disposal of the protein matters after they have entered the system through the portal vein. It has been seen that under the combined action of pepsin and trypsin the protein molecule is completely broken up into a number of smaller molecules, and what may escape the action of pepsin and trypsin is dealt with by erepsin before entering the blood. The protein substances once in the blood are utilised in the repair and restoration of the tissues, and a study of nitrogenous metabolism has shown that under ordinary circumstances the extent of this repair is probably not considerable, and it certainly has shown that whatever portion of the protein is so used must turn out a similar amount of degraded material from the tissues, or the outgo of nitrogen would be less than the income. What is the probable behaviour of protein in the body until the stage of urea is reached ?

Pflüger taught that the whole of the absorbed material must first be converted into protein before any destruction of it can occur ; in other words, that there is no short cut to urea excepting through the disintegration of the living cell. Voit held that the protein, when absorbed, is divided into two portions—one, the smaller, repairs wear and tear in the body, and he spoke of it as *tissue protein ;* the other circulates with the blood and lymph, and bathes the body cells, but does not form part of them. This is destroyed by the tissues with the liberation of heat and the formation of nitrogenous end-products, the chief of which is urea. This portion Voit described as the *circulating protein.*

The modern view does not differ greatly from that held by Voit. The split products of protein digestion, the amino-acids, now no longer protein, are reconstructed by the process of synthesis, and a protein formed allied to the body of the animal in which the change is taking place. This synthesis occurs either in the wall of the intestine or the liver, and serum albumin and globulin are thus formed. The observations on nitrogenous metabolism indicate that the whole of the split products are not so converted, only perhaps a small portion, while the balance not converted into tissue protein takes the short cut to urea after having been utilised as a source of energy. If the energy requirements of the body are less than the available energy, the non-nitrogenous portion of the protein surplus is stored up either as glycogen or fat. It has been shown experimentally that a dog may maintain its tissue nourishment, and even add to its body weight, when fed on the split products of pancreatic digestion, and this is a very important fact as bearing out the above views. We have seen that the urea is increased or diminished by increasing or reducing the protein supply in the food, while, on the other hand, the purin bodies excreted are not reduced by diminishing the protein in the diet. It has accordingly been suggested that the urea represents that portion of the protein which is not incorporated with the tissues, while kreatinin, xanthin, hypoxanthin, and uric acid represent the changes occurring in the body protein.

The difficulty in establishing nitrogenous ~~metabolism~~ equilibrium on a purely protein diet, and the cause of that difficulty, has already been dealt with. We are clearly shown from it that protein in the body splits up into a nitrogenous and non-nitrogenous portion, the former, as we have seen, being quickly got rid of, mainly as urea, while the latter is gradually oxidised. The percentage composition of protein is about $C_{53}, H_7, O_{22}, N_{16}$. The nitrogen having been cleared off, the carbon, hydrogen, and oxygen represent the non-nitrogenous moiety available after the formation of urea for the production of glycogen and perhaps of fat. Physiologists are not, however, agreed on the question of the formation of fat from protein, though the formation of glycogen is generally admitted. Most proteins possess what is known as a carbohydrate group, the exception being casein, which yields a reducing sugar on decomposition.

Nitrogen is a most expensive food-stuff, and economists in watching dietaries have repeatedly drawn attention to the unnecessarily nitrogenous, and therefore wasteful, nature of many diets for animals. We shall see that the bulk of the nitrogen in *fattening* animals passes away with the excreta, and only a small proportion of it stored up, but though the bulk has been excreted, the nitrogen has not been lost. It has passed through the system, and performed some function we cannot explain, and finally, from an agricultural point of view, it has conferred on manure its only value. Nevertheless, some diets are wastefully nitrogenous, and exact experiments on men have shown that they can be kept in health for months on a diet far poorer in protein than that generally accepted as necessary, and the same finding, within limits, holds good for animals. On the matter of food nitrogen many physiologists come into conflict with practical experience.

Theory says the quantity of nitrogen required is largely independent of muscular work ; practice says the harder the machine is worked the more nitrogen must be given. Theory says proteins are not the source of muscular energy, this being the function of non-nitrogenous food ; practice replies that may be so, but experience shows that the harder the work performed by an animal, the more strongly nitrogenous must the diet be, while the amount of the latter is only to be limited by the appetite. In this matter our personal experience places us entirely on the side of practice and opposed to theory. Why the hard-worked horse needs more nitrogen we are not prepared to explain. The suggestion that the machine works more easily and smoothly on a liberal nitrogenous diet, which stimulates metabolism, and so leads to increased oxidation, does not bring us much nearer to a solution of the problem. The fact remains that whatever may be the energy obtainable from starch and fat, this energy is in some unknown way directed by protein. All nitrogen over and above that required for repair is considered a wasteful or *luxus consumption*—a condition to which we by no means subscribe. That a wasteful consumption of protein occurs where horses are not fed in accordance with the work they are performing is undoubted. Under these circumstances the excess of nitrogenous material produces clinical effects ; we are able to recognise them in the liver disorders and diarrhœa of tropical climates, and lymphangitis, azoturia, and diarrhœa of temperate latitudes.

Doubtful and difficult of solution as many of the important points are in nitrogenous feeding, they are nothing in comparison with the problem of how the dead food-protein is converted into the living body-protein, and how the same kind of protein can be utilised in building up material so different in structure as bone and brain, muscle and fat, liver and skin.

The storing up of protein occurs, as we have seen, in young animals, and in working animals so long as the muscles are increasing in bulk. In making this statement it is necessary to remember that it does not exclude the daily repair of the tissues.

Whatever this may be—and it appears in the adult, as we have already seen, to be small—the embodiment of newly-arrived protein into the body tissues is associated with an equal output of worn-out material containing the same proportion of nitrogen, so that, though the nitrogen does not vary, the tissues do.

All true proteins are capable of being used as food, but when *albuminoids,* such as gelatin, are given they produce the same amount of urea as an assimilable protein, but the animal loses flesh. The gelatin story is interesting. Originally this substance held a high nutritive position in a diet, mainly owing to its chemical analysis and its close relationship to true protein. It took years to find out that from a dietetic point of view it was worthless as a nutrient. Something similar occurred in the feeding of horses. Bran yields an excellent analysis, and, in consequence, has frequently formed a prominent part of badly-arranged horse dietaries. As a matter of fact, the nitrogen in bran is worthless.

What we have learnt regarding nitrogenous food may here be summarised:

1. The body requires nitrogen; no diet is complete without it, nor can life be permanently supported in its absence.

2. The body having obtained its nitrogen, stores up the small amount required to replace wear and tear, and excretes the whole of the remainder mainly in the form of urea.

3. The assumption that the proteins are the source of muscular energy is incorrect; this is the function of non-nitrogenous food, yet increased muscular effort must be met by an increased nitrogenous ration. In some unknown way nitrogen directs the production of energy in the muscle machine.

Carbon Equilibrium.—This condition implies that the total carbon in the excreta is balanced by that received in the food. We have seen that an animal in nitrogenous equilibrium may be gaining or losing weight. This gain or loss must be fat. An attempt to establish carbon equilibrium on a purely protein diet, such as may be used for nitrogenous experiments, is difficult. We have seen how the system struggles on protein to obtain the necessary carbon, and that, in consequence, far more protein has to be consumed than is actually necessary to establish nitrogenous equilibrium. It has also been seen that much less protein food is necessary to establish nitrogenous equilibrium when a small quantity of fat or carbohydrate is added to the diet. The importance of carbon equilibrium is nothing like so great as that of nitrogenous, and this is explained by the fact that the amount of fat in the body varies within wide limits compatible with apparently perfect health.

Carbohydrates.

Non-nitrogenous Food. — The all-important feature in connection with the non-protein substances in food is that they are directly associated with muscular work. During work the intake of oxygen and output of carbon dioxide is immediately raised, and in the trained—that is, the 'fit'—animal, the increased intake is proportional to the work performed. The nitrogen of the body, it will be remembered, is unaffected, excepting during excessive work, and even then the amount bears no proportion to the work performed.

The whole of the **carbohydrate** matters found in food—viz., the starch, sugar, gum, and cellulose—must, as we have seen (p. 288), be first rendered soluble before they can enter the system. Further, they can only enter as some form of sugar, and are then stored up for future use as fat in certain depots, and as glycogen in the muscles and liver; while for present use they exist as dextrose in the circulating blood. The supply of carbohydrates is added to by the splitting up of proteins into a nitrogenous and non-nitrogenous portion; whether the non-nitrogenous portion of protein can form fat is uncertain, but it is undoubted that it forms glycogen. Carbohydrates are readily oxidised, as we have already seen. In this respect they are a great contrast to the fats. In dealing with the question of the 'respiratory quotient' (p. 118), it was explained that this fraction represented the relative amounts of carbonic acid produced and oxygen absorbed. The theoretical value of the respiratory quotient on a carbohydrate diet is 1, but with fats the volume of oxygen absorbed is greater than the volume of carbonic acid produced, and the respiratory quotient becomes 0·707. For example:

1 gramme (15½ grains) of carbohydrate requires 0·832 litre (50·8 cubic inches) of oxygen, and produces 0·832 litre (50·8 cubic inches) of CO_2.

1 gramme (15½ grains) of fat requires 2·8875 litres (176 cubic inches) of oxygen, and produces 1·434 litres (87·5 cubic inches) of CO_2.

In speaking of the respiratory exchange, attention was drawn to the fact that all the oxygen absorbed by the lungs was not returned as carbon dioxide; there was a missing portion. This **Oxygen Deficit** is greater when the amount of fat and protein in the diet is considerable, whereas it is smaller the more the carbohydrates preponderate in the food. The missing oxygen, in other words, is being employed in the oxidation of the hydrogen of fats, which, as we have seen, only possess in themselves one-eighth of the total oxygen required for the oxidation of their hydrogen to water. Similarly the proteins are short of oxygen for the oxidation of their hydrogen. These two sources, together with the oxygen used to oxidise the sulphur of proteins, account for the deficit.

Great interest attaches to the carbohydrates in the feeding of herbivora, as so little fat exists naturally in vegetable food. We have learnt that the carbohydrates are one of the sources of muscular energy, and with horses they are the chief source; this material is 'fired off' by the muscles during contraction; and under the influence of muscular work and starvation the whole store in the body may be used up. As the result of the oxidation of carbohydrates heat is generated, so that these substances supply not only energy but heat to the body. The seat of the necessary oxidation is, as we have seen (p. 129), in the tissues, and not in the blood; the tissues produce enzymes which break up the sugar with the formation of carbon dioxide and water; these enzymes are called into activity by the internal secretion of the pancreas. The amount of heat generated by the oxidation of sugar can easily be measured, 1 gramme (15½ grains) yields 4,100 calories, or 4·0 large calories of heat.* Oxidations are constantly going on throughout the life of the animal. During rest they are providing for the internal work and heat of the body, while during work, in addition to these, they furnish the muscular energy. The influence of carbohydrate as a protein sparer has already been mentioned; less protein is required with the food when carbohydrates are present in sufficient quantity. The value of carbohydrate in the diet was first established by Lawes and Gilbert, at a period when protein was considered the essential basis of all dietaries. Not only did these patient observers prove the absolute necessity of carbohydrates in the diet of fattening animals, but they showed that weight for weight the feeding value of starch and cane sugar was nearly the same.

The Fats.—The fat of animals is a compound of glycerin and fatty acids, the latter being stearic, palmitic, and oleic; the two former confer on fat its firmness, the latter enters into the formation of the fluid fats. The melting-point of fat depends upon the proportion of fatty acids in the mixture, the melting-point of olein being very low, and that of stearin and palmitin high. Olein is the solvent of the other fats. In milk fatty acids of the volatile series are present—butyric, caproic, caprylic, etc. As previously noted, there is very little fat in the food of herbivora—in fact, the amount is so small that in the fattening of animals fat is always specially added to the diet. It might hence be natural to conclude that the fat in the body is derived from the fat in the food, but this does not cover the whole ground; great stores of fat may exist in animals receiving a trifling amount of fat in the diet: a cow, for instance, may produce more fat in her milk than she receives in her food; a pig lays up more than exists in the fat plus protein contained in the diet; so that it is evident a something not fat can furnish it. This something is the carbohydrate which when in excess of requirements is stored up as fat in the permanent fat-reserve depots of the body, and subsequently doled out to the system as required. Perhaps also the non-nitrogenous portion of the protein molecule may contribute to fat formation, though this point is not settled. The storing up of fat is a physiological process, but under certain circumstances it may constitute a pathological condition. By its oxidation, which is referred to more fully at p. 364, fat furnishes heat and energy, and in this respect is of higher value than an equal quantity of carbohydrate; 1 gramme (15½ grains) of fat yields 9·3 *large* calories on oxidation. How it is prepared for oxidation is unknown; the fat as it lies in masses in the body cannot be oxidised until it is brought back into the blood and carried to the tissues, and it is suggested that the fat-splitting ferment, *lipase,* decomposes the fats into fatty acids and glycerin, in much the same way that the same ferment splits the fat in the intestinal canal before absorption. Should this be the case, the lipase regulates the supply of fat to the blood. It has been stated that in the blood the fat derived from the intestines on absorption is changed into an unknown substance, which is soluble, easily reversible, filtrable, dialysable, and so transported into the tissues.* It is, therefore, assumed that what applies to fat when taken up from the intestines holds good for that taken up from the body.

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* A *large* calorie is the amount of heat necessary to raise 1 kilogramme (2·2 pounds) water 1° C. (1·8° F.), and is conveniently named a kilo-calorie.

There are certain fat-reserve depots natural to the animal, and on which, under ordinary circumstances, little or no drain occurs; such are found beneath the peritoneum, around the kidneys, in the mesh of the omenta, and surrounding the base of the heart. It is only under the influence of starvation that the fat in these places is drawn on. The chief means to induce the laying on of fat is a liberal diet and freedom from exercise and work. The farmer feeding for beef or mutton understands the value of keeping the animals as quiet as possible, and recognises also that there are certain breeds which have a distinct predisposition to store up fat. Further, he learns how necessary it is to introduce animals gradually to a fattening diet until toleration is established, and he knows from practical experience that he will not succeed in fattening within a reasonable time unless to the diet of carbohydrate and fat he also adds proteins liberally. The measure of the diet is that of the animals' appetite; they can never eat enough to please the feeder, who cheerfully accepts the heavy initial outlay, as he knows the subsequent saving in time effected. The obesity aimed at with 'show' cattle, sheep, and pigs is a pathological condition repugnant to common sense, and the outcome of a barbarous fashion. The laws regulating the fattening of animals are mentioned at p. 368.

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* 'Recent Advances in Physiology and Biological Chemistry.' Edited by L. Hill, M.B., F.R.S.

The consensus of opinion is in favour of castration as facilitating fattening, though this view has not stood the test of scientific inquiry. It is conceivable that if it has some such effect, it may easily be explained on the ground of greater freedom from excitement. It is quite certain that geldings have no greater disposition to accumulate fat than mares, and if castration favoured fattening there would be no need for that constant striving after fatness instead of 'fitness,' which is so characteristic of all who have charge of horses. There are, of course, some animals which have a tendency to store up fat and others which never do any credit to their 'keep,' but this is an individual peculiarity not explained by castration.

The fat of horses is soft and of sheep hard; that of cattle occupies a middle position. Each animal has fat of a certain melting-point to store up, and whether this be derived from oil, carbohydrate, or food-fat, makes very little, if any, difference. In the fattening of the herbivora it is considered that carbohydrates are better fat producers than food fat. The form in which the fats in food are stored up has been made the subject of many experiments: a dog fed on a hard fat converts it into canine fat, which is soft; cattle fed on fluid fats, such as linseed oil, convert them into hard body fats; still, experiments go to show that foreign fats used for feeding may, if given in sufficient amount, be recognised in the tissues. Oil-cake and linseed oil may produce an oily milk, owing to the increased amount of olein, and dogs constantly fed on mutton-fat may accumulate this type of fat in the body. Pigs receiving too large a proportion of oil in the diet accumulate a soft fat, which boils away in cooking; and swedes will produce the same result. It is said that green food, hay, and carbohydrates, produce a hard body fat, while grain feeding, such as oats, conduces to a soft fat.

Fats, like carbohydrates, exert a sparing action on proteins, and for this reason a fat animal takes longer to starve to death than one which is less fat.

Inorganic Food.—The **salts** in the body perform important functions in connection with secretion and excretion; as Foster expresses it, they direct the metabolism of the body, though how they do so is unknown. To their presence is due the normal composition of the body fluids and tissues, for they regulate the water-flow from blood to tissues and *vice versa*. Proteins which are freed from salts are quite altered in their essential characters, while the part taken by the salts of the body in blood-clotting, rhythmical contraction of the heart, irritability of muscle and nerve, milk-curdling, and growth is of supreme importance. The distribution of the salts throughout the structure is remarkably regular, sodium being found in the blood plasma, potassium and iron in the red cells, sulphur in hair and horn, potassium in sweat, sulphur in protein, and lime in bones, etc. Animals fed on a diet which is as far as possible rendered free from salts soon die. When a deficiency in salts occurs, the body apparently for some time draws on its own store, and then nutritive changes follow. These are more likely to show themselves earlier with young than with adult animals, but the influence of inorganic food on the nutrition of the skeleton is little understood.

The chief salt used by herbivora is potassium, whilst sodium is used by carnivora. Both carnivora and herbivora obtain in their natural diet a sufficiency of these salts, though there is a general impression that the wild herbivora long for sodium. It is quite certain that under the conditions of domestication horses can be kept in perfect health without receiving any sodium chloride, other than that naturally contained in the food, and the amount of this in vegetable substances is small. The iron required by the blood is probably furnished in some organic combination. It is evident that the daily quantity of salts required must depend upon the age of the animal, young growing animals requiring more than adults.

Storage of Tissue.—Every diet must contain the food principles we have been considering, viz.:

Protein.
Fat or *carbohydrate*, or both.
Salts.

It is interesting to learn in what proportion these are stored up in animals being fattened, also the amount of food required for a definite increase in weight, and the rate at which that increase occurs. This is shown in the following table from the classical experiments of Lawes and Gilbert:

PROPORTION OF FOOD PRINCIPLES STORED UP FOR EVERY 100 POUNDS INCREASE OF BODY WEIGHT.

	Protein.	Fat.	Salts.	Amount of Dry Substance in Food required to produce 100 Parts Increase in Weight.	Weekly Increase in Body Weight.
					Per Cent.
Oxen -	9·0	58	1·6	1,109	1·0
Sheep -	7·5	63	2·0	912	1·75
Pigs -	7·0	66	0·8	420	6 to 6·5

The table shows that in all cases the chief increase in body weight is due to the deposition of fat. The ox lays on the most protein, the sheep stores up the largest amount of salts, the pig puts on the most fat, and fattens, not only on the smallest amount of food, but in the shortest time. The table on p. 343 shows that in a given weight of body substance, animals passing from the lean to the fat conditions lose nitrogenous and mineral matter ; in oxen and sheep the fat increases nearly twice, and in pigs fully twice as much as in the lean state. The water diminishes and the total dry substances increase in passing from 'store' to fat condition.

Water.—The amount of water found in the tissues of animals is very constant, and, as may be seen from the table on p. 343, the total body water in animals in different conditions of fatness is shown to be very similar. The muscles of creatures as far removed as the pig and the snail, the ox and the lobster, contain 78 to 79 per cent., and other tissues are equally uniform. We have just seen that in fattening animals the body loses water, the tissues in consequence becoming drier (see table, p. 343).

Under the influence of rest and work varying quantities of water are lost, and in hot weather the loss is still further increased. It has been calculated that a man may lose water at the rate of 5 per cent. of his body weight on a hot day, and that muscular work in hot weather may increase the output of water as much as six times ; but we are not aware of any exact experiment on this question on animals, though we know practically that the loss of water is considerable. Of the total water received in the food or consumed, the bulk passes away by the kidneys ; during work a considerable amount is lost by the skin and lungs, and less in consequence passes by the kidneys.

The very constant proportion of water in the tissues shows that the consumption of excessive amounts of fluid does not lead to storage. Adjustments are readily effected, and the excess of fluid in the blood is rapidly got rid of. All animals withstand a deficiency of water badly ; the horse is probably the weakest in this direction, and shortage of water is far more immediately serious for any horse than shortage of rations. A thirsting animal dies when it has lost 10 per cent. of its body weight in water, though 50 per cent. of its protein and the whole of its fat will disappear before death from starvation ensues. A man may avoid putting on weight by keeping himself short of fluid, and horses will rapidly lose condition by having their water supply limited. Without sufficient water neither rumination nor intestinal digestion in herbivora can go on ; the contents of the rumen of the ox and of the colon and cæcum of the horse must be kept fluid, and much of the water consumed is devoted to the purposes of digestion. Further, the blood must be kept fluid and concentration avoided; a concentrated blood draws on the tissues for fluid, but later on, this source dries up, and unless dilution of the blood be effected, death is only a matter of time, and with horses undergoing severe exertion a very short time before complete collapse occurs.

Starvation.—When an animal is starved it lives on its own tissues; in the herbivora the urine becomes acid, hippuric is replaced by uric acid, and the secretion becomes transparent. We have seen (p. 351) that the elimination of nitrogen by the starving animal at first falls rapidly, then gradually. During starvation the carbon dioxide excreted falls in amount, and the oxygen absorbed becomes reduced, though not in proportion to the fall of carbon dioxide. If water be given, life is considerably prolonged; Colin records a case where a horse receiving water lived thirty days without food. It is notorious that herbivora, though they lose less protein during starvation than carnivora, do not withstand starvation so well; nor need we go so far as a starvation experiment to ascertain this fact. When men and horses are being hard worked, the loss in condition amongst the horses sets in early, and is extremely marked for some time before the men show any appreciable muscular waste.

Horses have been known to live without food or water for as long as three and dogs for four weeks; but it is said that if horses have suffered fifteen days' starvation, the administration of food after this time will not save them.* Colin records an experiment where a horse weighing 892 pounds died after thirty days' starvation, only being allowed 2½ pints of water per diem. The animal was nourished on its own tissues, the daily loss in weight being 5·9 pounds, which must be considered as exceptionally small. Dewar† records two remarkable instances of the length of time sheep will withstand starvation; in one instance eighteen sheep were buried in the snow for six weeks and only one died. In the second case seven sheep were buried for eight weeks and five days, and all were recovered alive, and eventually did well.

In some very accurate experiments on a starving cat, it was shown that the principal loss occurred in the fat, 97 per cent. of which disappeared in thirteen days. The following table shows the percentage of dry solid matter lost by the tissues:

Fat	97·0 per cent.
Spleen	63·1 ,,
Liver	56·6 ,,
Muscles	30·2 ,,
Blood	17·6 ,,

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* If the writer's memory serves him, this period also applied to man during the Great Famine in India several years ago.

† *Veterinarian*, May, 1895.

The loss in the glandular organs was very heavy; next followed the muscles, and then the blood. The heart muscle and central nervous system suffered no loss; evidently their nutrition was kept up at the expense of other tissues of less importance. Old animals bear starvation much better than young growing ones, as their requirements are smaller.

Cause of Body Waste.—The work of the body may be described as internal and external. By *internal work* we refer to respiration, the action of the heart, mastication, peristalsis, glandular secretion, hydrolysis, fermentation, warming of ingesta, cleavage and synthesis during absorption, the production of animal heat, all of which are sources of expenditure of energy; by *external work* is understood those movements of the muscles which support or transport the body. Every diet given to an animal must take these two factors into consideration. The *ration of subsistence* is the minimum diet necessary for the internal work of the body without incurring loss of weight, the animal, of course, doing no work; the *ration of labour* furnishes the actual muscular energy employed during work. The changes undergone by food in providing energy as heat and motion fall principally, if not exclusively, on the non-nitrogenous elements. This has been settled beyond all doubt.

During work the heart and respirations are quickened, the horse sweats, and a larger volume of air is warmed in the lungs. All this means a loss of heat to the body. In addition, the muscles produce heat as the result of contraction—in fact, every process seems to tell essentially on the non-nitrogenous elements of the body, which is the explanation why carbohydrates are so necessary.

The **Energy yielded by Food** has been ascertained by burning the substance in a calorimeter and measuring the amount of heat given off. In this way the potential energy of protein, fat, and carbohydrate has been ascertained. Every 1 gramme (15·432 grains) of water in the calorimeter raised 1° C. (1·8° F.) is called a heat unit; by this method of investigation it has been found that—

1 gramme of average protein evolves, approximately, when oxidised, 5,770 heat units,* or 5·7 *large* calories.†

1 gramme of fat evolves, when oxidised, 9,300 heat units, or 9·3 *large* calories.

1 gramme of carbohydrate evolves, when oxidised, 4,100 heat units, or 4·1 *large* calories.

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* One heat unit or small calorie is the quantity of heat necessary to raise 1° C. in temperature 1 gramme of water.

† For definition see footnote, p. 358.

Proteins, unlike carbohydrates and fats, are not completely oxidised in the body, inasmuch as the nitrogen they contain reappears in the excreta in the form of urea. The complete oxidation of 1 gramme of urea yields 2,523 calories (or 2·5 kilo-calories),* which must be subtracted from the value given above for the potential energy of proteins in order to ascertain the energy-value of proteins actually available by the body. Speaking approximately, 1 gramme of protein gives rise to ⅓ gramme of urea; hence the heat of combustion of proteins must be diminished by one-third of 2,523 = 841 calories, before we apply the data to the body. This gives us a heat-value for average proteins of 4,929 calories, or 4·9 kilo-calories, as based on purely physical determinations. This, according to Rübner, is too high. By modern methods of calorimetry he has shown that the actual heat energy obtained from protein in the animal body is about 4·1 kilo-calories.

It is by the oxidation of food-stuffs in the body that heat is generated, and the table above shows how largely this heat is derived from the carbohydrates and fat. The heat value of food-stuffs is easily calculated on the basis of the figures above given, and the modern method of considering dietary sufficiency is to compare the heat energy in the food with the energy needs of the living body. The law of the conservation of energy applies to the living body.

There are chemical changes in the body, like hydrolysis, which give rise to but little heat—in fact, heat may be lost in connection with digestion processes—for instance, the warming of food, and especially that of the water consumed. That this loss of heat is considerable is rendered evident to the senses of those engaged in horse management. Nothing is more common, especially in winter, than for the horse to shiver some time after watering. The temperature of the fluid has to be raised some 60° F., and 4 or 5 gallons of cold water consumed in twenty-four hours robs the body of a great deal of heat.

But there are sources of loss which are not so evident, and the **respiration calorimeter** shows that the actual value of food for herbivora is less than its theoretical fuel value. The explanation lies in the fact that so much of the latter is consumed in those processes necessary to the preparation of vegetable food for the use of the body—for instance, mastication, rumination, fermentation, putrefaction, peristalsis, etc. Coarse fibrous feeding substances, both hay and grains, are a further source of loss, owing to the extensive fermentation they have to undergo in order to be of any use. In fact, no comparison can safely be made between the energy value of the diet of herbivora and that

* For definition see p. 358.

of the more concentrated foods used by man until all feeding substances used for animal nutrition have been submitted to direct experiment in the animal body within the respiration calorimeter.

The application of this apparatus to problems in animal feeding is well illustrated by determining the income and output of energy of the steer previously referred to, where the diet was insufficient. In the observation recorded on the *balance of matter* at p. 349 the steer had lost 49·2 grammes of protein, and 259 grammes of fat. The respiration calorimeter shows how this loss affects the *balance of energy*. In the following table the income and outgo of the energy is shown:

	Income.	Outgo.
	Calories (Large).	Calories (Large).
Hay - - - - - -	13,035	—
Linseed-meal - - - -	1,824	—
Fæces - - - - - -	—	6,432
Urine - - - - - -	—	853
Methane - - - - -	—	984
Hair, etc. - - - - -	—	88
Heat produced by steer - -	—	9,215
	14,859	17,572
Loss of energy by steer - -	2,713	—
	17,572	17,572

An analysis of the table shows that the total calories in the diet was 14,859, and of these 8,357 appeared unused in the various excreta. The balance of 6,502 was all that was left to support the vital activities, shown in the table as equal to 9,215 calories. To meet the food deficit, the body tissues had to be drawn upon to furnish 2,713 calories, and these were obtained by the oxidation of 49·2 grammes of protein and 259 grammes of fat, the loss shown in the balance of matter at p. 349.

The Amount of Food Required.—The minimum amount of food required by horses during idleness has been determined experimentally. The amount required for work cannot be fixed with precision, owing to individual variations. What is sufficient for one is insufficient for another. Still, diet tables for working horses have been constructed on the basis of the mean amount found by practical experience to be necessary.

Subsistence Diet.—This is the diet necessary for the internal work of the body, the weight of the animal remaining unchanged.

It represents the minimum amount of food required by horses doing no work. Grandeau and Leclerc kept three horses for a period of from four to five months on a diet consisting of 8 kilogrammes (17·6 pounds) of meadow hay. The animals led a life of idleness, with the exception of receiving half an hour's walking exercise daily. The 17·6 pounds of hay furnished as a mean 7·02 pounds of dry digestible organic matter for every 1,000 pounds of body weight. The 7·02 pounds of organic matter contained 0·538 pound of digestible proteid. The subsistence diet for three horses for twenty-four hours was, therefore, as follows for every 1,000 pounds of body weight:

Protein - -	0·244 kilogramme	0·538 pound
Non-nitrogenous	2·946 kilogrammes	6·482 pounds
	3·190 kilogrammes	7·020 pounds

This amount of hay (7·020 pounds) contains the following elements:

Carbon - -	1·619 kilogrammes	3·563 pounds
Hydrogen - -	0·175 kilogramme	0·385 pound (6·16 ounces)
Oxygen - -	1·357 kilogrammes	2·986 pounds
Nitrogen - -	0·039 kilogramme	0·086 pound (1·376 ounces)

Assuming the correctness of Grandeau's observations, we may accept the above amounts of carbon, hydrogen, and nitrogen as approximately representing a horse's requirements for twenty-four hours during idleness, the animal neither gaining nor losing weight. The ratio of nitrogen to carbon in the above diet is 1 : 41; the ratio of the proteins to the non-nitrogenous fats and carbohydrates is 1 : 12.

From a table furnished by Grandeau and Leclerc, it would appear that no matter what the nature of the diet may be, horses require between 7 pounds and 8 pounds of dry *digestible* organic matter daily for every 1,000 pounds of body weight in order to maintain nutrition during idleness. The following is the table referred to:

Diet.	In the Ration.	Amount digested.	Amount for 1,000 Pounds of Body Weight.
	Pounds	Pounds.	Pounds.
Hay alone - - - - -	14·08	6·09	7·02
Maize and oat straw - -	11·57	8·33	8·22
Maize, oats, hay and straw -	9·48	7·30	7·50
,, ,, ,, ,, -	9·49	6·74	7·45
Oats alone (crushed) - -	8·59	6·41	7·02

In some German experiments made by Wolff on the subsistence ration, 8·3 pounds of digestible dry organic material were found necessary to maintain the body weight, and from this the digestible fibre, 1·6 pounds, was deducted, as in the experience of Wolff the fibre digested by horses was of no value as sustenance either at work or rest. In the writer's observations on the essential diet for horses, it was found the body weight could be maintained on 12 pounds of hay.

The essential diet presupposes that the food possesses a sufficient proportion of digestible proteins. In one of Grandeau's experiments a horse received 33 pounds of wheat-straw per diem, which furnished 13 pounds of digestible matter daily (nearly twice the amount actually required), but this diet only supplied 0·157 pound of digestible proteins, or less than one-third of the minimum, the result being the horse died from starvation.

The essential diet for an ox weighing 1,000 pounds is, according to the experiments of Wolff, 0·5 pound to 0·6 pound of protein, and 7 pounds to 8 pounds of non-nitrogenous matter reckoned as starch. The ratio of nitrogenous to non-nitrogenous matters is as 1 : 14. According to the same authority, sheep require a relatively larger essential diet, owing to the growth of wool and its accompanying fat—viz., for 1,000 pounds of live weight 0·9 pound of protein and 10·8 pounds of non-nitrogenous matter, the ratio being 1 : 12.

The **Fattening of Animals for Food** may not be regarded as a physiological process, nevertheless, the fundamental principles involved are purely physiological. The whole agricultural world is indebted to the life labours of the late Sir John Lawes and the late Dr. Gilbert for a knowledge of the true principles of fattening. We have seen how their work led to the Liebig doctrine of the physiology of dietetics being overthrown. In one of the public statements made by Lawes on the subject of these experiments he explained the method of inquiry adopted :*

> 'Writers on agricultural chemistry and physiology have generally assumed that it is chiefly the proportion of the nitrogenous or so-called flesh-forming substances contained in them which determines the comparative value for feeding purposes of different foods. The coloured diagram before you will enable you to judge whether or not this supposition is justified by the practical experience of feeding. This diagram has been constructed by the animals themselves. They know nothing about nitrogenous or non-nitrogenous constituents, digestible or indigestible cellulose, and so on ; but are gifted with an unerring instinct which enables them, not only to distinguish between substances which are and are not food, but also to select from a variety of food-stuffs those which are most suitable. . . . In the experiments to which the diagram refers, as well as

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* 'The Chemistry of the Feeding of Animals,' a lecture delivered before the Royal Dublin Society, March, 1864, by John Bennett Lawes, F.R.S.

in many others, the plan has been to select foods containing very different proportions of nitrogenous and non-nitrogenous compounds ; in fact, some contained two or three times as much nitrogen as others. We have, then, given to one set of animals a small fixed amount of food daily containing a low percentage of nitrogen, and allowed them to take as much as they chose of another food, different in composition in this respect. To another set we have given a limited amount of food, rich in nitrogenous compounds, and allowed the animals to take *ad libitum* of a different description of food and so on. In this way they have been enabled to fix for themselves the limit of their consumption of nitrogenous and non-nitrogenous constituents respectively, according to their wants. The diagram shows the results of such experiments. . . . It is perfectly clear the animals were guided in the amount of food they consumed by the amount of non-nitrogenous, and not by that of the nitrogenous constituents supplied.'

Regarding the function of the nitrogenous and non-nitrogenous portions of food, the following statement was made :

1. The comparative feeding value of stock food depends more upon the proportion of the digestible non-nitrogenous substances they contain than upon their richness in nitrogen compounds ; but the richer the food in nitrogen, the more valuable will be the manure.

2. Of the non-nitrogenous constituents of food, starch and cane sugar have, weight for weight, nearly equal feeding values ; malt sugar has probably rather a lower value than either cane sugar or starch ; digestible cellulose in moderate proportion has, for ruminant animals, probably nearly the same value as starch ; and fat or oil has probably about two and a half times the value of starch for the purpose of respiration or the storing up of fat in the body.

The following were the general conclusions arrived at by Lawes and Gilbert on the fattening of animals :

During the fattening process the water, nitrogenous matter, and salts of the body decrease in a given weight of the animal, and the fat greatly increases (see table, p. 343).

The amount of dry substance in food required to produce a given weight of increase is larger in the ox than in the sheep, and larger with the sheep than with the pig ; for instance—

To produce 100 parts increase in weight, the ox required 1,109 parts dry substance of food.

To produce 100 parts increase in weight, the sheep required 912 parts dry substance of food.

To produce 100 parts increase in weight, the pig required 420 parts dry substance of food.

The dry substance of the food of the ox contains a larger proportion of indigestible matter than that of the sheep, and that of sheep more than that of pigs :

In 1,109 parts dry substance of food of ox 404·4 parts were indigestible and excreted.

In 912 parts dry substance of food of sheep 291 parts were indigestible and excreted.

In 420 parts dry substance of food of pig 70 parts were indigestible and excreted.

Oxen require from five to six, and sheep from three to four, times as long to add a given proportion to the weight of their bodies as pigs.

The greater part of the nitrogenous and mineral matter of the food is recovered from the urine and fæces, and the greater part of the non-nitrogenous matter is lost by respiration and other exhalations, a much smaller proportion being retained in the increase or voided in the excreta.

For a given amount of increase in weight produced, oxen excrete considerably more substance and expend more in respiration, etc., than sheep, and sheep very much more than pigs :

For 100 parts increase in weight, the ox excretes 404·4 parts in urine and fæces, and 636 parts by respiration.

For 100 parts increase in weight, the sheep excretes 291 parts in urine and fæces, and 548·5 parts by respiration.

For 100 parts increase in weight, the pig excretes 70 parts in urine and fæces, and 65·7 parts by respiration.

For a given weight of *dry* substance consumed, oxen void more as excreta than sheep, and sheep more than pigs, but oxen respire less than sheep, and sheep rather less than pigs :

Of 100 parts of dry substance, the ox excretes by bowels and kidneys 36·5, and by respiration 57·3.

Of 100 parts of dry substance of food, the sheep excretes by bowels and kidneys 31·9, and by respiration 60·1.

Of 100 parts of dry substance of food, the pig excretes by bowels and kidneys 16·7, and by respiration 65·7.

In proportion to a given weight of animal within a given time, oxen both consume and respire less *dry* substance of food than sheep, and sheep very much less than pigs, but each class of animal voids almost identical amounts of dry substance in the excreta :

For 100 parts live weight per week, the ox consumes 12·5 parts dry substance of food, excretes by bowels and kidneys, 4·56 parts, and by respiration 7·16 parts.

For 100 parts live weight per week, the sheep consumes 16·0 parts dry substance of food, excretes by bowels and kidneys, 5·10 parts, and by respiration 9·62 parts.

For 100 parts live weight per week, the pig consumes 27 parts dry substance of food, excretes by bowels and kidneys, 4·50 parts, and by respiration 17·74 parts.

The following were the amounts of food required by different classes of animals to produce a given increase in live weight :

Oxen : 250 parts oil-cake will produce 100 parts increase in weight ; 600 parts clover chaff will produce 100 parts increase in weight ; 3,500 parts swedes will produce 100 parts increase in weight.

Sheep : 250 parts oil-cake will produce 100 parts increase in weight ; 300 parts clover chaff will produce 100 parts increase in weight ; 4,000 parts swedes will produce 100 parts increase in weight.

Pigs : 500 parts barley-meal will produce 100 parts increase in weight.

Pathological.

Disorders of nutrition occur with every departure from the normal condition, though much more apparent in some disorders than others.

Fever.—The tissues are readily broken down in supplying fuel for the increased metabolism which is giving rise to the abnormally great production and loss of heat ; both the fats and proteins suffer, and in some disorders it is remarkable how rapidly wasting occurs the moment the reserve is used up. In acute lung cases this is very obvious—in a fortnight the patient may be a wreck. The increased nitrogenous metabolism which this indicates suggests an increased secretion of urea, but exact work in this direction is still much needed. During fever there is an increased production of CO_2, and absorption of oxygen ; uric acid is formed by the herbivora, and the urine becomes acid.

Marked muscular waste may occur in the absence of fever ; anything which causes a drain on the system, such as internal parasites, tuberculosis, internal growths, etc., may reduce the animal to little more than a skeleton. Starving, underfeeding or overworking of animals are obvious causes of metabolic change, while defective teeth in horses are a frequent cause of the same.

The food supply may be deficient in proteins or carbohydrates, or both, or there may be an excess. Disorders from the latter cause are very evident in the horse. **Lymphangitis** and **hæmoglobinuria** are diseases of the horse intimately associated with overfeeding and idleness, and have no parallel in any other animal. An excess of salts in the food may be productive of considerable trouble. One form of intestinal calculus in the horse is due to the amount of ammonio-magnesium-phosphate existing in the bowel through feeding too largely on bran.

Broken Wind is referred to at p. 152 as having its origin in errors in dieting and management, such as a bulky and innutritious food supply, or heavy work on a distended stomach. Apart from these there may be other disorders of nutrition responsible for this condition, for even under good management the production of the disease is not entirely controlled, though very greatly reduced.

Local loss of nutrition, such as occurs in lameness, is referred to at p. 349.

CHAPTER XII

ANIMAL HEAT

Oxidations.—In dealing with internal respiration on p. 129, we learnt the fundamental fact that the oxidations of the body do not occur in the blood, but in the tissues. By means of these oxidations heat is produced, and the substances which are oxidised—viz., protein, fat, and carbohydrate—have already been studied in the chapters on digestion and nutrition. The manner in which oxidations are carried out in the tissues is not clearly understood—in fact, it is by no means decided how oxidations occur outside the body. The view that oxygen directly unites with the substances oxidised is no longer accepted, for it is known that oxidations do not occur in the absence of watery vapour. In spite of the fact that oxidations within and without the body are very similar, and in their results practically identical, the conditions under which each is produced are not the same, the great dividing line being the relatively low temperature at which oxidations in the body are effected. It is probable that oxidations in the tissues occur under the influence of enzymes and not directly by the presence of oxygen, for it can be shown that, provided sufficient oxygen be supplied, any further increase does not affect the rate of oxidation. We have had before us evidence showing the existence of tissue ferments capable of splitting fat, of oxidising sugar, of converting sugar into glycogen, glycogen into sugar, and of acting on proteins; all of these may be isolated from the body tissues, and are known as *intracellular* enzymes. Other evidence can also be adduced of the existence of tissue ferments, by the fact that living substance removed from the body with suitable precautions will be found to digest itself; this is known as *autolysis*. It is supposed that the enzymes of the body stimulate the oxygen to activity; such enzymes have been called **oxidases,** and have been found both in plants and in the animal body. They have not, however, been found in connection with the oxidation of protein, fat, or carbohydrate, though this may yet be demonstrated. An oxidase effects oxidation in the presence of oxygen; enzymes which only act in the presence of hydrogen peroxide are called *peroxidases*. It is considered probable that the splitting up of food-stuffs by ordinary hydrolytic ferments is the first stage in the process, and this is followed by the action of oxidases on the split products. To the oxidases is due the formation of carbon dioxide, water, etc., and the production of heat; the heat formed in the body by the oxidation of fat and carbohydrate is probably the same in amount as is formed in their combustion outside; the nitrogenous moiety of the protein, however, is not fully oxidised, inasmuch as urea and other waste products carry away with them at least one-third of the available energy (p. 365). How the heat formed in the body is distributed, maintained and lost, must now be considered.

The Body Temperature.—One important division of the animal kingdom is into warm-blooded and cold-blooded animals. A *poikilothermal*, cold-blooded, or animal of changeable temperature is one in which the body temperature depends upon its external surroundings. When these are cold the bodies of such animals are cold, being about a degree or so higher than the medium in which they are living. Such a condition exists in reptiles, fish, etc. A *homoiothermal*, warm-blooded, or animal of practically constant temperature, is one in which the body temperature is independent within wide limits of the temperature of the medium in which it is living: whether this be high or low makes practically no difference. Between these two come a class partaking of the characters of each, *hibernating* animals which during the summer are homoiothermal, and during the long winter sleep are poikilothermal.

The temperature of the body is not uniform, the interior is warmer than the exterior, and the blood in the interior veins is warmer than that in the corresponding arteries. The blood in the veins leading from a gland in a state of activity has a higher temperature than the blood which enters the gland. In the animal body the hottest blood is found in the hepatic veins, while the blood in the posterior vena cava is hotter than that in the anterior. There is also a difference in the temperature of the blood in the right and left hearts; it is generally considered that the blood in the right heart is the warmest, though Colin found that in the horse the blood of the left side was generally the hottest. The brain has also a high temperature. The practical aspect of the question is that the interior of the body is hotter than the exterior. A surface temperature does not indicate the temperature of the body, which for clinical purposes should be taken in the rectum. With the air at freezing-point there may be as much as 3·0° C. (5·4° F.) difference in temperature between the rectum and the thin skin of the breast in the horse, while at the same external temperature the limbs of this animal, which are naturally cold, in consequence of the underlying tissues having very little vascularity, may indicate 25·4° C. (44° F.) difference between the pasterns and the rectum.

The Normal Temperature of Animals.—The wide differences which exist in the normal temperature of animals of the same class is remarkable. The following observations were made principally by Siedamgrotzky.

Horse: The temperature varies between 38·0° to 38·2° C. (100·4° to 100·8° F.). Age has a slight influence, being somewhat higher in extreme youth and lower in old age.

Cattle: The normal temperature is from 38·7° to 38·8° C. (101·8° to 102° F.). Wooldridge* places the mean at 38·5° C. (101·4° F.), and gives the variations at 38° to 39·3° C. (100·4° to 102·8° F.).

Sheep: In these animals the greatest variation in temperature occurs, viz., from 38·4° to 41·0° C. (101·3° to 105·8° F.). Probably the majority of temperatures lie between 39·7° to 40·2° C. (103·6° to 104·4° F.). The cause of the variation is unknown.

Swine: The average temperature is 39·0° C. (103·3° F.), varying from 38·2° to 40·7° C. (100·9° to 105·4° F.).

Dog: The dog is liable to important variations, depending on the external temperature. According to Dieckerhoff, it varies from 37·4° to 39·4° C. (99·5° to 103° F.). Other observers place it at 38·2° to 38·4° or 38·7° C. (100·9° to 101·3° or 101·7° F.).

Variations in Body Temperature.—A rise or fall in body temperature does not necessarily imply an increase or diminution in the production of heat. To demonstrate increased heat production it is necessary to show that the metabolism is increased, that more oxygen is absorbed, and more carbonic acid produced. In all animals there is a daily variation in temperature, the lowest records being obtained in the early morning, 2 to 4 a.m., the highest in the evening, 6 to 8 p.m., after which the temperature falls during the night. These variations are due to metabolism; during rest the metabolism sinks, the tide is low, while during activity it rises. The temperature of the young animal is higher than that of the adult, while the temperature of animals in temperate climates living in the open is lower than those under cover; in the case of the horse as much as 1° F. difference in temperature has been registered under this condition. In the tropics the temperature of animals exposed in the open, during the day, is higher than that of animals under cover. Other causes of variation in temperature will be considered presently. The thermometer does not tell us the amount of heat formed in the body, it only indicates the outcome of a difference between the heat produced and the heat lost. These important points must now be studied.

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* 'The Temperature of Healthy Dairy Cattle.' See Proceedings of the Royal Dublin Society, vol. x., part iii., 1905.

Heat Production.—The oxidations occurring in tissues, and leading to the production of heat, have previously engaged our attention ; the bulk of these changes occur in the skeletal muscles, in which four-fifths of the daily heat are generated, and in active glands such as the liver. The heat furnished by glandular activity is amply demonstrated in the liver, though certainly not in all secreting glands. The temperature of the blood in the hepatic veins is higher than in the portal, higher even than in the aorta. It was shown by Bernard that in the dog, while the portal vein was registering 39·6° C. (103·5° F.), the blood in the hepatic veins was 41·2° C. (106·3° F.). Heat is formed during muscular contraction. Experiments carried out on the external masseter muscle of the horse showed that during contractions the thermometer registered 2·8° C. (5·0° F.) higher than in the same muscle at rest. As the blood streams out of the muscle its temperature is higher than that in the corresponding artery, and in this way the whole mass of blood would have its temperature raised were it not for mechanisms by which the heat is dissipated. But the excessive production of heat is not always compensated by a sufficiently rapid loss, and a high temperature may in consequence be produced as the result. This is a most important point in connection with working horses. In the case of man a rise of 1° to 1·5° C. in body temperature may occur as the result of work. In the horse half an hour's trotting may raise the temperature from 0·4° to 1·4° C. (0·7° to 2·7° F.) above the normal; the amount of rise is largely a question of ' condition '; temperatures of 40° to 41° C. (104° to 105° F.), and even higher, after hard work, especially in a hot sun, are not uncommon. With rest the temperature falls in the course of a few hours, the mechanism for getting rid of heat being able to cope with it; as heavy a fall as 4° F. in two hours has been recorded (Willis). With animals unfit for work through want of condition the temperature may take longer to fall, or even remain above the normal sufficiently long to be designated febrile ; ' fatigue fever ' is not unknown in man. Fever may be due either to excessive production of heat or defective dissipation. In the above case it is probable that both factors are at work.

The act of feeding, which involves increased muscular activity, not only immediately, but subsequently in the muscles of the whole alimentary canal, raises the temperature of the body.

In the dog the maximum is reached from six to nine hours after a meal, during which time from 20 to 25 per cent. more heat is produced. In the horse, according to Siedamgrotzky, the temperature as the result of feeding may rise 0·2° to 0·8° C. (0·4° to 1·4° F.); but, according to this observer, there is no similar rise in the ox; and Wooldridge found not more than 0·3° F. in dairy cattle. That heat is formed during the masticatory processes we have already seen from the observations on the masseter muscles of the horse; but the mechanisms for regulating heat in the body are such that a rise of anything like 1·4° F. as the result of feeding must be regarded as exceptional.

Influence of the Nervous System on Heat Production.—The muscles of the skeleton are not always actively contracting, yet heat is always being formed in them. The heat produced in resting muscles is formed as the result of *Muscle tonus*—viz. the contracted condition of the muscles essential to posture. There is also in operation, even with the most trifling movement, an antagonism to muscular contraction. For example, the flexors of a limb cannot contract without the extensors being thrown into a condition to oppose the movement. Heat production in muscles is under the control of the nervous system. If an animal be poisoned with curare the motor end-plates are paralysed, in consequence less heat is formed in the muscles, and the temperature sinks; in fact, the animal becomes for the time being practically cold-blooded, the body temperature rising and falling with the surrounding temperature. The same condition may be produced by dividing the spinal cord in the neck, by which means the motor nerves are cut off from the muscles, and the animal becomes practically cold-blooded. In chloroform narcosis heat production is also greatly interfered with; in prolonged operations this should be borne in mind and the loss of heat guarded against. Shivering is a physiological process associated with the production of heat to compensate for a loss. The shivering which occurs with horses after being watered is caused by the consumed water abstracting heat from the tissues in order that its temperature may be raised to that of the body. The 'freshness' of a horse on a winter's morning is the outcome of nervous impulses instinctively started with the object of generating more heat in the body.

Heat Centres and Heat Nerves.—Apart from contraction, it is believed that muscles are the seat of a quiescent heat production under the influence of the nervous system, and that chemical changes resulting in the formation of heat are generated as the result of nerve impulses. Experimental injury to the corpus striatum, the so-called '*heat puncture,*' causes an increased production of heat, which may last for some time without, apparently, causing the animal any inconvenience. Heat centres have also been located in other portions of the brain, such as the optic thalamus, septum lucidum, etc., and in the spinal cord. By some it is supposed that this extra heat production takes place in the liver, but the balance of opinion inclines to locating it in the muscles. No special set of thermogenic nerves is known to exist, and no special heat-regulating centre has ever been discovered ; but there is good reason for believing that through the nervous system the physiological oxidations in the muscles are reflexly regulated, and heat produced according to requirements. Rubner, who has specially studied the question of animal heat, considers that chemical regulation does not perform the same important function with man as with animals, in consequence of his custom of protecting the surface of the body with clothing.

Heat Loss.—Unless some conditions exist in the body for the regulation of the temperature, the heat resulting from metabolic activity would continue to rise steadily until it accomplished the destruction of the animal, and that this is no mere figure of speech is evident from the fact that a horse produces sufficient heat during idleness to raise the body to boiling-point in less than two days. In order to maintain the temperature at a constant point, heat production and heat loss must balance. This balance may be struck either by heat production being diminished, or as the result of increased loss of heat. The temperature of the body may rise either in consequence of an actual increase in metabolism, or through difficulties in getting rid of heat. The processes by which, within narrow limits, accurate and prompt adjustment is made is known as **heat regulation**, or **thermotaxis.**

If cold water be poured on a hot body, the body is cooled ; if the surface of a heated body be wetted and the water allowed to evaporate, the body is cooled. If a cold body be placed in contact with one which is hot, heat is lost. And processes somewhat similar to these are occurring in the animal body.

1. By *Radiation and Conduction* heat is lost to surrounding bodies, provided, of course, that they are at a lower temperature than that of the animal ; if the surrounding medium is hotter than the animal's body, then heat is gained instead of being lost. The natural or artificial covering, be it hair, wool, or clothing, checks the loss by radiation and conduction, as in a dry condition they are bad conductors of heat. When wet, however, they are good conductors, and a considerable amount of heat is lost from sweating or rain. Clothing acts by imprisoning a larger amount of warm air, the air so confined being a bad conductor.

2. By *Evaporation* from the skin the sweat is converted into vapour and heat is lost, the rapidity of the process depending on the humidity of the air and its rate of movement. If the air be saturated, no evaporation occurs from the skin, and, consequently, no heat is lost. The value of evaporation as a source of heat-loss in the horse is considerable, probably higher than the figure fixed for man—viz., 14·5 per cent. of the total—but no data are available. Evaporation is constantly occurring; when the amount of sweat is small it is evaporated as fast as it is produced, and this is referred to in the chapter on the skin as insensible perspiration. The sensible perspiration is that which is not evaporated as rapidly as it is produced, and is the source of a much greater loss of heat.

3. *Evaporation from the mouth and nostrils, warming of inspired air, and vapourising of water from the lungs.* The former is a very valuable means of heat loss in those animals which do not sweat from the general surface of the skin; the moist nose and open mouth of the dog are good examples of the principle, and in a much smaller degree the bedewed muzzle of the ox. The warming of the inspired air and the vapourising of water from the lungs are most important sources of heat loss in those animals which do not sweat. The panting respirations of the dog, and of cattle and sheep in 'show' condition, are simply a means of cooling the body by warming a larger volume of air, and offering a moist surface for evaporation. No evaporation can occur when the air is saturated with vapour.

4. *By the urine and fæces* a loss of heat is incurred in warming the food and water to the temperature of the body. The amount of loss thus brought about must be relatively considerable, especially in winter; the abstraction of heat after drinking may be so great as to cause shivering; experiment shows that drinking a pailful of water at 50° F. may cause the body temperature of the horse to fall 0·5° to 0·9° F. A diet of roots, containing as they do 80 per cent. water, is a heavy source of heat loss with cattle in winter, though both in the case of the water consumed and the succulent food ingested, no actual loss of heat occurs until these are excreted as urine and fæces.

The heat lost by conduction, radiation, and evaporation, is greater in small than in large animals, as small animals have a relatively greater surface exposed in proportion to their body weight (see Fig. 107). A dog of 66 pounds weight will lose 79·5 per cent. of his body heat by radiation and conduction, and 20·5 per cent. by the evaporation of water; whereas a dog weighing 8 pounds will lose 91 per cent. by radiation, etc., and 9 per cent. by water evaporation.

Bulk of body is a safeguard in large animals against sudden loss of heat. All warm-blooded animals living in the sea are bulky. It takes considerable heat-loss to lower the body temperature of a horse 1°, so that small animals in which, as we have seen, the cooling surface is relatively greater than in large animals, must be able to increase rapidly their heat production. Heat production varies as the cube of the body volume, heat-loss varies as the square of the body surface.

The skin as a source of loss of heat is largely controlled by the nervous system. Through the vasomotor nerves the vessels of the skin are constricted or dilated ; when the vessels are constricted the skin becomes pale (though this may not be seen, owing to hair and pigment) and the blood is thrown upon the internal viscera, where it is additionally shielded from loss. In consequence the skin becomes cold and the loss of heat less, not merely as the result of the lessened radiation, but chiefly as the outcome of the diminished evaporation. When the vessels are dilated the skin becomes flushed and hot, the veins stand out with blood, and a large amount of heat is lost. This vasomotor action is an automatic reflex act, as also is the nervous control over the sweat-glands, by which more or less water is poured out on the surface of the body and heat lost by its evaporation. This nervous control is normally set in action by changes in the temperature of the surroundings.

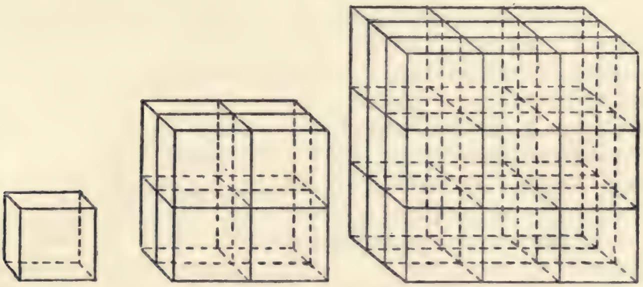

FIG. 107.—DIAGRAM TO ILLUSTRATE THE RELATION BETWEEN VOLUME OR WEIGHT AND SURFACE (WALLER).

The volumes are 1	8	27	cubic centimetres.
The weights are 1	8	27	grammes.
The surfaces are 6	24	54	square centimetres.

That is to say, their ratio of increase is 1 4 9.

The loss of heat is influenced by the thickness of the natural covering, its colour, etc. The loss of heat from a rabbit after shaving off the fur is one and a half times greater than before shaving. Sheep before shearing excrete less CO_2 and more H_2O than the same sheep after shearing. White rabbits lose

75 per cent. less of the heat lost by black or grey, for white not only absorbs less heat during the day, but loses less heat at night. Grey horses are better suited to the tropics than any other colour, and black horses least of all. The black skin of the negro protects the deeper tissues from the sun's rays, from which it might be argued that black horses in theory should stand exposure to a tropical sun better than grey, but a grey horse has a black skin, and the pigment prevents the rays from penetrating. Loss of heat from the body surface can be experimentally produced by varnishing the skin, so that the animal dies from cold unless rolled up in cotton-wool (see p. 312).

Influence of Heat and Cold.—A moderate degree of cold applied to the external surface of the body increases the production of heat, due to increased oxidations. This results, as we have seen (p. 376), from reflex impulses discharged through the motor nerves. At the same time the appetite is increased to meet the extra demand, and foods rich in fat are instinctively sought after by man. The same should be observed in the feeding of animals, and an increase allowed in the food to meet the extra oxidations, fat, if possible, forming part of it. The body will stand a considerable degree of cold, but a continuous fall in external temperature cannot be withstood ; a point is reached where the rate of heat production is below that of heat-loss, and the animal dies from cold. Conversely the body is adjusted to withstand a moderately high external temperature ; the heat of Arabia or India, which renders surrounding objects, such as metal, too hot to hold, and the very birds to sit with drooping wings and wide-open mouth, is borne with impunity by the acclimatised horse ; the heat-regulating mechanisms do not allow the external heat to be stored up. A continuous rise in external temperature cannot be long borne, and a point arrives when the heat kills, for when the discharge of heat from the body ceases, as it does when the surrounding air goes above a certain point, it becomes stored up, and heat-stroke follows. A far higher temperature can be borne when the air is dry than when moist, as evaporation from the surface practically ceases in a moist atmosphere. Men have been exposed to a temperature of 127° C. (260° F.) for a few minutes without ill effects, and with no elevation of the body temperature. When air has its humidity increased by 1 per cent. it raises the loss by radiation and conduction 32 per cent., while an increase of 25 per cent. in the humidity of the air is equal to an increase of 2° C. in the external air. At a temperature of 31° C. (88° F.) in an atmosphere saturated with vapour the regulating mechanism of man is exhausted, and a rise in body temperature occurs. Horses taken from cold to hot latitudes have to learn to compensate, and until they do so a febrile rise in body temperature, with increased respirations and pulse, will occur as the result of standing in a hot sun, even though doing no work. This passes away with acclimatisation, but increased respirations on a hot day are always evident even in animals of the country.

The loss of body heat among animals lying out at night is partly prevented by the fatty covering to the peritoneal cavity, which saves undue conduction of heat. Wet, combined with exposure, causes a more important loss of heat than mere cold. It has been shown from exact observations on man that a limb clothed in wet flannel lost 34·4 per cent. more heat than the same limb in dry flannel. Animals never look so wretchedly miserable as after a night of cold rain ; under the conditions of active service, a cold, wet night is certain to kill off the most debilitated.

A physiological resistance to cold can be obtained by training ; the body learns to regulate its loss and production of heat, and this brings us to a consideration of the interesting practical point of the necessity of clothing for animals, especially for horses, in a state of domestication. Some animals, such as the horse, ox, and sheep, are born fully developed and clothed ; in a few minutes they pass from a temperature of between 101° to 105° F. within the womb of the parent, to perhaps freezing-point on the bare ground. The power of regulating their temperature is fully established, and in a very short time this is assisted by muscular movements of the limbs, which are learnt very quickly ; the gambols of young animals serve some other purpose than that of mere lightness of heart. If healthy, cold has no effect on these young creatures, provided the parent is able to supply sufficient nourishment. There are other animals, such as newly-born pups, kittens, rabbits, and certain birds, such as pigeons, which are born blind, helpless, and more or less naked ; they cannot move, are unable to regulate their temperature, and if taken from the maternal warmth their body temperature steadily declines and they die from cold. In these the capacity for regulating body temperature does not develop for some little time after birth, and until locomotion becomes possible.

Effect of Low Temperatures.—We have seen, then, that the young of the horse comes into the world prepared by its heat-regulating mechanism to deal with the question of external temperature, and as time goes on this is supplemented by an extra growth of hair for winter use and a lighter covering for the summer. If no interference with the coat be practised it is undoubted that no extra covering of any kind is required during the coldest weather, and even where the natural covering is of the lightest, as with the thoroughbred horse, it is sufficient for the purpose. The thoroughbred brood mares of this country, once they go to the stud, live in the open for the remainder of their lives, and never wear a blanket. And practical experience tells us that this may be gradually imposed on all horses with impunity, even those which have been kept in hot stables. Coughs, colds, and inflammatory chest affections, usually attributed to cold, are practically unknown among horses living in the open, even during the coldest weather, and it is easy to show that these diseases are largely the result of the artificial conditions under which working horses have to live.

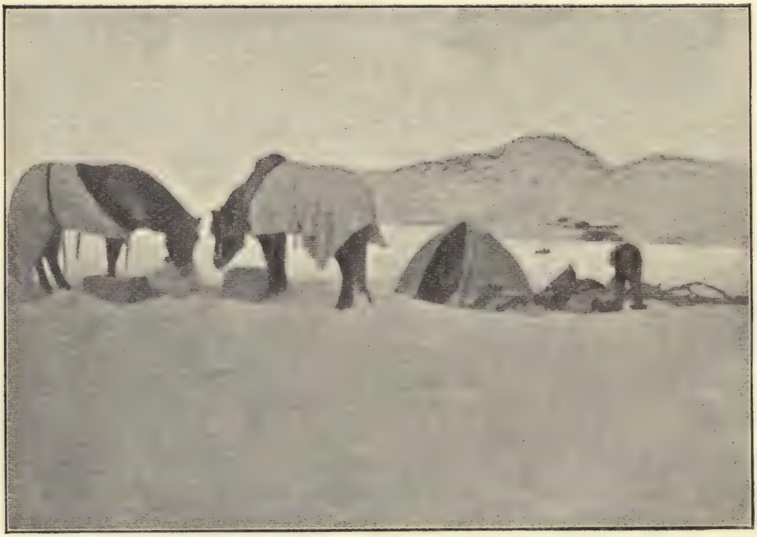

Fig. 108.—Ponies living in the Open in the Arctic Circle, at 45° F. below Zero (Jackson).

Jackson* has proved that the law of adaptability which applies to men living in the Polar regions applies with equal force to horses; for two and a half years he kept horses at 80° north latitude. During this time the thermometer never rose higher than 11° F. above freezing, while 70° to 80° F. below freezing were common temperatures. During the sleighing expeditions these animals lived in the open, and wore one blanket, which, as may be seen in Fig. 108, found its way where most blankets get, under the hind-feet. At the time the photograph was taken the animals were in a temperature of 45° F. *below zero* at night—viz., as far below freezing-point as summer heat is above it. It is interesting to note they did not suffer, and Major Jackson informs the writer they were never frost-bitten, and never had a cough or cold. Exposure to a low temperature renders the body sensitive to a rise in the thermometer. Jackson, in the work previously noted, tells us that the July temperature of 8° above freezing-point made it feel like midsummer, and far too warm! Conversely, living in a high temperature renders the body very sensitive to a fall in the thermometer.

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* 'A Thousand Days in the Arctic,' F. G. Jackson.

If a part be persistently protected against air-currents, it becomes sensitive to exposure; if it be habitually exposed, a considerable degree of cold can be borne with impunity. Our faces are never covered, and only the hands by some. People who wear no gloves do not complain of cold hands, and it takes a winter of Arctic intensity to make the face feel cold. Women naturally wear far less clothing than men, and in consequence, under the necessities of fashion, they exhibit a remarkable degree of tolerance to cold. The bare-footed child is not conscious of cold feet, nor is he, or the hatless man, marked out as a subject for catarrh. We have the evidence of Darwin* that unclothed man can withstand the most tempestuous climate in the world outside the Arctic Circle. The natives of Tierra del Fuego at the time of Darwin's visit wore nothing; newly-born infants were exposed like their parents. These people did not die from cold, in spite of the rigours of the climate; their heat-regulating mechanisms were evidently perfect.

Clipping.—Now that the clipping of horses can be done expeditiously and cheaply, fashion decrees that the horse shall be clipped all over. Limited clipping is absolutely necessary for working horses, but there is no necessity to remove all the hair of the body. Strange to say that when this is done horses do not feel the effects of being robbed of their natural cover, even though no clothing be supplied. After twenty-four hours they do not feel the cold any more than a man does who has had his hair closely cut; nevertheless, they are losing, in consequence, more heat, and therefore require more food. It is economical to clothe the horse which is wholly clipped. Siedamgrotzky observed the effect of clipping on the temperature of horses. He found that the temperature rose after the operation, and fell to normal about the fifth day. It was observed that clipped horses had during exercise a higher rectal temperature by 1·8° F. than unclipped horses, and the return to normal was more steady and regular with them than with unclipped. The rise in temperature after clipping may be due to vasomotor action; less blood being in the skin, more will find its way to the viscera—viz., to parts of the body which have a naturally high temperature, the result being that the total mass of blood has its temperature raised. Another way of accounting for the rise in temperature after clipping is by supposing that an actual increase in the production of heat occurs ; this may be due to stimulation of the skin influencing the heat-forming mechanism. Colin clipped a horse on one side of the body, and not on the other ; the *subcutaneous* temperature in the stable was :

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* 'Voyages of the *Adventurer* and *Beagle*.'

Clipped Side.	Unclipped Side.	Difference.
86·9° F.	95° F.	8·1° F.

The animal was now taken out into cold air at 3° below freezing-point.

	Clipped Side.	Unclipped Side.	Difference.
In 30 minutes the subcutaneous temperature was - - -	85·1°	94·1°	9·0°
2½ hours later - - - -	79·9°	95·0°	15·1°
1 hour ,, - - - -	83·3°	95·5°	12·2°
1 ,, ,, - - - -	85·1°	96·1°	11·0°

The cooling of the clipped side is very marked, the temperature continuing to fall for three hours, while the slight fall in the temperature of the unclipped side was restored to normal in three hours.

Hibernation.—The effect of a fall in the temperature of the bodies of animals is to produce a depression of metabolism. This is well seen in some mammals, such as the dormouse, which sleep all the winter, during which time they live upon the store of fat laid up in the tissues during the summer. Owing to their depressed metabolism this store is found sufficient to keep them alive, though they wake up at the end of the winter mere skeletons. On waking up the body temperature rises by bounds to the normal, the animal then returning to the condition of an ordinary warm-blooded animal, until the recurrence of the next period of hibernation. As to the causes of this remarkable phenomenon we know but little. It is not confined to only one class of animals, since it occurs in mammals, amphibians, reptiles, etc. No purely anatomical differences suffice to explain why some animals hibernate and others do not. External cold is usually assumed offhand to be the initiating factor, assisted possibly by the lessened food supply at the approach of winter. But some other more recondite cause than either of these must exist, since marmots may sometimes hibernate in the summer, dormice will hibernate even if kept warm in the winter ; cold will not necessarily cause an animal to hibernate except at the appropriate season, and *severe* cold may even arouse a hibernating animal from its state of torpor.

The **Amount of Heat produced** by animals depends upon the rate of their metabolism and the surface area of their bodies ; the latter factor determines the loss of heat, and hence its production if the temperature of the body is to be kept constant. A large animal produces actually, but not relatively, more heat than a small one ; a small animal, as has been previously stated, has a greater body surface relative to its weight than a large animal, and in this way its loss is more rapid. As heat production must balance heat loss, the small animal must lose more heat, and therefore produce relatively more heat, than a large animal.

In the following table the body surface has been calculated by a formula, and the heat given off per *unit of surface* is seen to be very close in all animals :

	Weight in Kilogrammes.	Calories in Twenty-four Hours.	
		Per Kilogramme.	Per Square Metre of Surface.
Horse	441·000	11·3	948
Man	64·300	32·1	1,042
Dog	15·200	51·5	1,036
Rabbit	2·300	75·1	917
Mouse	0·018	212·0	1,188

The heat produced is measured as heat-units or calories—viz., the amount of heat required to raise 1 gramme of water 1° C., known as the 'small calorie,' or the amount required to raise 1 kilogramme of water 1° C. This is the large calorie sometimes spoken of as the 'kilogramme-calorie.'

The method by which the heat given off by a body is ascertained is by means of a **calorimeter** (Fig. 109). This is a chamber with a double wall containing air or water, which absorbs the heat given off, say, from an animal in the chamber. This chamber is contained within another, and the two separated by non-conducting material in order to prevent loss of heat by radiation. The weight of the water in the calorimeter is known, and the extent to which its temperature is raised during the experiment ascertained ; a simple calculation shows the number of calories given off during the observation. The temperature of the animal's body before and after the experiment shows whether the loss of heat has been made good or not, or whether, on the contrary, the body has produced more heat than it got rid of. By the process of calorimetry the heat value of food is also ascertained. In the Respiration Calorimeter described at p. 346, the heat given off from the body is compared with the heat obtainable from the food, and both the material and energy expenditure ascertained. The amount produced per hour for every kilogramme (2·2 pounds) of body weight is given by Colin as follows :*

Horse	1·643	large	calories.
Sheep	2·6	,,	,,
Dog	4·0	,,	,,

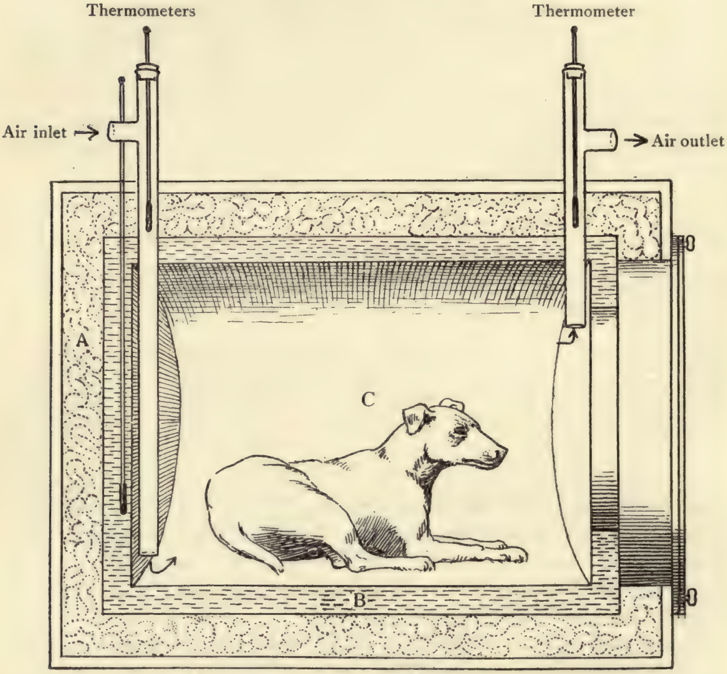

FIG. 109.—CALORIMETER.

The animal is resting in the chamber, which has a double wall containing water. There is an air inlet and outlet to the chamber, and delicate thermometers for ascertaining the temperature of the water, and of the incoming and outgoing air. The whole is placed within another chamber and surrounded by packing of non-conducting material.

A, Outer insulating chamber ; B, middle water-chamber ; C, inner chamber.

Assuming that the living body and water have the same density, the horse produces per unit of time enough heat to raise by 1° C. a mass of water fifty times greater than that of his body.

A horse loses, according to Colin, 20,684 large calories per diem, or sufficient heat to raise 4,550 gallons of water 1·8° F., or to raise 44 gallons from freezing to boiling point. Wolff, quoted by Tereg, gives a table showing the heat lost per diem by cattle, horses, sheep, and pigs, for every 500 kilos (1,100 pounds) of body weight :

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* These results are higher than those obtained by calculation and tabulated on the previous page. Colin's figures are based on Boussingault's experimental inquiry into the income and expenditure of the body.

Horse at moderate work	24,500 large calories.
,, hard work	37,200 ,, ,,
Ox resting, and on moderate diet	18,600 ,, ,,
Sheep, with fine wool	27,700 ,, ,,
Pigs, fattening	35,000 ,, ,,

Post-mortem Rises of Temperature are frequently observed, and some of the observed temperatures have been remarkably high. The writer recorded in the horse 109° F. between the liver and diaphragm. The explanation afforded is that metabolism is still occurring in the tissues, but since there is no circulation to carry the heat away the temperature of the part rises.

Pathological.

The actual processes occurring in fever are not known. It cannot be definitely stated whether the increase in temperature is due to an increased production of heat or to a disturbance of the mechanism by which the loss of heat is regulated—probably both causes are in operation. It has been supposed by some that fever may be due to the action of bacterial poisons on the heat-centres, and it has been stated that cultures which produce fever in the intact animal no longer do so on division of the pons, which cuts off the basal ganglia heat-centre from the rest of the body. Others have considered that, though the nervous mechanism is at fault in some cases, in others the activity of the heat-forming tissues themselves is at fault. This view receives some support from the action of agents employed in the treatment of fever ; whereas some, like quinine, act on the tissues, others, like antipyrin, appear to produce their effects through the nervous system, particularly on the vessels of the skin. Fever leads to a marked increase in the metabolism of protein. This is shown by an increase in the output of nitrogen ; uric acid appears in the herbivora. Ammonium salts of organic acids and kreatinine are increased, and kreatine, which normally does not appear in the urine, may now be found. The absolute amount of urea is greater than normal, but its proportion to the other urinary nitrogenous substances may be relatively less. Fever is probably a protective mechanism in infective processes ; nevertheless, high temperatures effect great damage to the body-tissues, especially the heart-muscle, and methods which control temperature appear clinically to give the best results in treatment.

CHAPTER XIII

THE MUSCULAR SYSTEM

The muscular system is the largest in the body, the skeletal muscles alone representing 45 per cent. of the body weight.

The regulation of the blood supply, the movements of the skeleton, the contraction of the heart, and the transport of the ingesta along the intestinal canal, are all examples of muscular movement, and, further, they are examples of different kinds of movement ; the slowly moving intestinal canal is very different from the active skeletal muscles, and these, with their long periods of activity and rest, are greatly in contrast with the rhythmical movements of the heart.

Structure of Muscle.—There are three varieties of muscle in the body :

1. Voluntary, skeletal, striped, or red muscle.
2. Involuntary, pale, smooth, or unstriped muscle.
3. Heart muscle.

The *voluntary muscles* are generally in large masses known as ' flesh,' and their function is to move the skeleton. The muscle mass consists of bundles, the bundles are composed of smaller bundles, the smaller bundles are made up of fibres. The fibre of a muscle does not run the length of the bundle ; on the other hand, a primitive fibre is only about 4 or 5 centimetres (1½ to 2 inches) in length, and of microscopic thickness—viz., $\frac{1}{500}$ inch on an average. The fibre is as a rule unbranched, its ends are rounded, and it is enclosed within a sheath, or *sarcolemma*. The contents of the fibre consist of a semifluid, contractile substance, marked with alternate dark and light bands (Fig. 110). Each fibre is made up of bundles of *fibrils* or *sarcostyles*, between which is a coarse network or reticulum, known as *sarcoplasm*. The sarcostyles show the light and dim bands seen in the fibre. Through the middle of each light stripe is a transverse line known as Dobie's or Krause's membrane (Fig. 111). The dim band is the sarcous element ; each is separated by a line known as Hensen's, and one portion of the dim band, together with a light band, form a *sarcomere;* a series of sarcomeres form a sarcostyle. The sarcous element is filled with longitudinal canals or pores, which communicate with the bright end of the sarcostyle; when the muscle contracts, the bright or clear part of the contractile substance passes into the pores, and for the time being is almost lost to view, while the sarcomere shortens and widens; when the muscle relaxes, the clear substance emerges from the pores, and the sarcomere lengthens and narrows. It is generally believed that the fibril constitutes the contractile substance of the fibre, the sarcoplasm being of a nutritive nature. When the bands are examined by polarised light, the dim band is found to be doubly refractive (*anisotropous*), while the light band is singly refractive (*isotropous*).

In some muscles, like those of the heart and diaphragm, the sarcoplasm exists in relatively large amounts; such muscles are deeper in colour than ordinary skeletal muscle, they contract more slowly, and may be said never to tire. Striped muscle may therefore be dark as in the case of the heart, full tinted as in the ordinary skeletal muscles of the larger herbivora, or pale bloodless-looking structures, such as are found in the rabbit and some fishes. In the rabbit both pale and red fibres may be mixed up in the one muscle. These pale striated muscles exhibit structural differences from ordinary striated muscle.

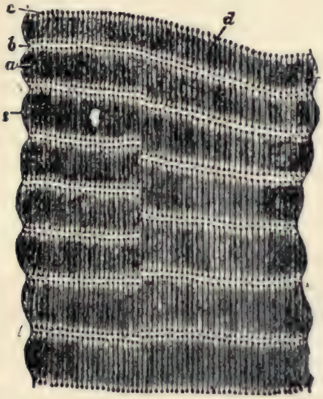

FIG. 110.—LIVING MUSCLE OF INDIA-BEETLE (HIGHLY MAGNIFIED) (SCHÄFER).

s, Sarcolemma; *a*, dim band; *b*, light band; *c*, row of dots: bright stripe, which appears to be the enlarged ends of rod-shaped particles, *d*, but in reality represents expansions of the interstitial substance (sarcoplasm).

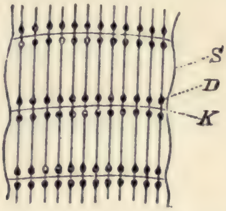

FIG. 111.—PORTION OF LEG MUSCLE OF INSECT TREATED WITH DILUTE ACETIC ACID (SCHÄFER).

S, Sarcolemma; *D*, dot-like enlargement of sarcoplasm; *K*, Krause's membrane. The sarcous elements have been swollen and dissolved by the acid.

The *nerve* supply to muscle is both motor and sensory: through the *sensory nerves* the brain is made acquainted with the position of the body and the condition of muscular tension. This involves the existence of a special **muscle sense** which plays such an important part in locomotion. In the muscles this sense is represented by special bodies generally found near tendons, called *neuro-muscular spindles*; these are from $\frac{1}{8}$ to $\frac{1}{3}$ inch in length, and $\frac{1}{125}$ inch in width; each spindle is of muscle surrounded by a sheath, and has a sensory nerve entering it at one end. Nervous structures known as the *tendon organs of Golgi*, also exist in the tendons at their junction with the muscle fibres; they consist of spindle-like bodies connected with one or more fine medullated nerve fibres. These nerves are in communication with a portion of the brain which is devoted to the 'muscle sense.' The ordinary degree of sensibility in muscle is not very great unless the part be cramped or inflamed, though pain is caused when they are cut into. By means of the *motor nerves* the muscle is supplied with impulses which, originating in the brain, passing thence along the spinal cord, and emerging by the ventral roots, reach the skeletal muscle concerned, and so bring about contraction. Division of the motor nerves, or interference with their function, causes paralysis of the muscle or muscles supplied by them. Each motor nerve enters the primitive fibre about its centre, and terminates in a special organ known as an *end plate*. By means of *curari* this end plate may be paralysed, in which case stimulation of the nerve leads to no muscular response in consequence of the block, though the muscle itself remains irritable, and readily responds to direct stimulation.

The question of the nerve supply to muscles will receive fuller consideration when the subject of 'muscle sense' is dealt with in the chapter on the Senses (Section IV.). It will also engage attention in Chapter XIV. on the Nervous System, when the extremely important subject of *reflex inhibition* is discussed. It will suffice here to point out that the nerves conveying impulses which pass from muscles, which later on will be known as *afferents*, are numerous, while the nerves conveying impulses which pass to muscles, known as *efferents*, are limited to the transmission of those impulses which stimulate contraction. There is no set of efferents to a muscle which prevent or control contraction, though obviously this is as important as the excitatory impulses which initiated it. How this difficulty is overcome is a matter of future consideration.

Masses of material built up on the lines described above are intended for the transport of the body, for which purpose they are united to the skeleton either by tendons or by the direct insertion of their own fibres. In the muscles of the limbs the tendon attachment is the most usual, wherever, in fact, the parts are exposed to great strain. There are certain muscles in the machine where the strain on them is so considerable that tendinous material is intimately mixed up with the muscular tissue ; this is well seen in the masseters, the muscles of the back, forearm, and thigh. During progression the muscular strain is enormous ; for example, in the canter and gallop a weight equivalent to that of the whole body is propelled by one foreleg (see chapter on Locomotion). In the horse provision is also made for the muscles of the limbs being rested without necessitating the animal assuming a recumbent position ; the mechanism will be explained when dealing with the locomotion system, but by means of it an animal can sleep standing, and may remain standing for some weeks without serious suffering.

Muscle Antagonism.—Every muscle, or group of muscles, possesses an antagonist, and though the antagonist may be equal in size, this is not always the case, as, for example, the great difference between the bulk of the muscles which close the jaw as compared with the trifling size of those which open it. The grouping of voluntary muscles in locomotion, so as to ensure co-ordination, is a question to be considered later, in the chapters dealing with the Nervous System, the Senses, and Locomotion. The interest which is here attached to antagonistic muscles is connected with the fact that it is this antagonism which keeps the muscles of the body slightly on the stretch, so that if one be cut across it gapes in consequence. This elastic tension ensures that no time is lost in a muscle coming into action, as there is no slack to take up ; the muscle stands as it were at full cock.

Involuntary, or Pale Muscle, is not found in masses as is the red, but in thin sheets, which in places, such as the bloodvessels, are only of microscopic thickness. Pale muscle is employed throughout the whole length of the digestive canal from the stomach to the rectum ; it is also found in the bladder, uterus, spleen, and bloodvessels. In none of these places is the sharp, short, active contraction of skeletal muscle required ; slow, steady, deliberate movements are essential in the digestive canal ; slow, steady, expulsive movements are necessary in the bladder and uterus, and even in the bloodvessels, where, as we have seen, the muscular tissue acts the part of a tap, it is sufficient if this tap is turned on or turned off slowly and steadily. When we come to study muscular contraction, it will be seen how rapidly the wave passes along a voluntary, and how slowly along an involuntary, muscle.

In structure pale muscle consists of nucleated spindle-shaped cells, dovetailed, and held together by a cement substance ; it is through the medium of this cement substance that the wave of excitation passes from cell to cell, thus forming a great contrast to red muscle, where, as we shall see, the whole contracts not by the spread of the stimulus from one fibre to another, but as the result of all the fibres being stimulated simultaneously. There are nerves and ganglion-cells in abundance in pale muscle; the nerves, which are chiefly non-medullated, form a fine plexus, with the ganglion-cells placed at the junctions of the plexus. It is probably due to these cells that involuntary muscle continues to contract when all connections with the centre are destroyed, though some physiologists see reason for thinking that the contraction of pale muscle may be carried out just like that of heart muscle—viz., as a self-acting mechanism, independent of any nervous connections.

The nerve supply of involuntary muscle is peculiar, and presents a great contrast to that of red muscle; whereas the latter only receives one variety of motor supply, pale muscle receives two—viz., one set of fibres which *stimulates* contraction, and another which *inhibits* it. Both sources are derived from the sympathetic system, which again is in great contrast to the arrangement of the nerve supply to red muscle.

Heart Muscle, as we have seen (p. 31), is in structure both red and striated, nevertheless it is involuntary; the fibres are characterised by being formed of branched, nucleated, quadrilateral cells, while the sarcolemma is absent. The contraction of the heart is primarily dependent on the properties of its muscle substance, though the automatism is carefully directed by nervous mechanisms (p. 48).

Muscular Contraction.—This apparently simple act is extremely complex, and will require to be dealt with in some little detail.

Muscles are tissues possessed of **irritability** and **contractility**—viz., they possess the power of responding by a movement to the application of a stimulus. The normal stimulus is effected through the motor nerves under the control of the brain or spinal cord, but of the nature of this stimulus we are ignorant. A coarse reproduction of it can be effected by pinching, pricking, chemical, thermal, or electrical stimuli, applied to either the nerve or the muscle itself, and to all these the three varieties of muscle are responsive. When a muscle contracts, in addition to becoming shorter and thicker, it undergoes changes in its extensibility, elasticity, and temperature; there are also alterations in its electrical condition and chemical composition. These can all be studied by employing a muscle of the frog, which retains its irritability for a long time after removal from the body. Such a muscle suitably prepared is known as a *muscle-nerve preparation,* and with certain modifications what is found to occur in this as the result of contraction, occurs also essentially in the living mammalian muscle.

The muscle most usually and conveniently employed for investigating the phenomena of muscular contraction is the *gastrocnemius* of a frog, dissected out in such a way as to leave its upper tendon connected with a piece of the femur and its lower tendon, the *tendo Achillis*, intact though free. At the same time care is taken not to sever the connection of the muscle with its motor nerve, the *sciatic*, which is dissected out for some considerable distance back towards its point of exit from the spinal canal, the central end being, if desired, left connected to a portion of the spinal cord enclosed in a piece of the lower end of the spinal column. The muscle is then suspended by fixing the remains of the femur in a clamp ; a small S-hook is then attached to the tendo Achillis. This muscle - nerve preparation and its arrangement as above described is shown in Fig. 112.

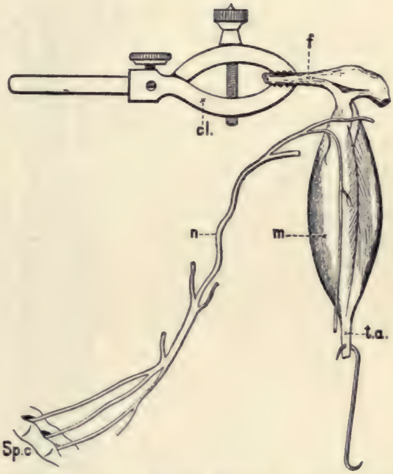

FIG. 112.—A MUSCLE-NERVE PREPARATION (FOSTER).

m, The *gastrocnemius* muscle of a frog ; *n*, the *sciatic* nerve dissected out back to *Sp c*, the lower end of the spinal canal ; *f*, femur ; *cl*, clamp ; *t a*, *tendo-Achillis* with S-hook attached.

For purposes of experiment the clamp is fixed inside a small chamber with glass sides to prevent the drying of the muscle and nerve ; this is effected by placing a few pieces of wet filter-paper inside the chamber. The sciatic nerve is laid over a pair of electrodes connected by wires to binding-screws outside the chamber ; by this means any desired electrical stimulus may be applied to the nerve. A thread attached to the hook in the tendo Achillis passes through a hole in the floor of the moist chamber, and is connected with a horizontal lever free to move in a vertical plane, a small weight being hung under the lever to give the muscle the 'load' necessary for its efficient contraction. The free end of the lever is then brought to bear against the vertical surface of some recording apparatus, usually a cylindrical drum, covered with smoked paper, made to rotate by clockwork about a vertical axis.

An inspection of Fig. 113 shows at once that if the drum of the recording instrument alone rotates, the end of the lever connected to the muscle must trace out a horizontal line on the smoked surface. If the drum is stationary and the muscle is made to contract, the lever will trace a vertical line. If now the muscle is made to contract while the drum is rotating, these two lines are compounded into a curve whose ordinates at each point of the curve and whose general shape give us exact information as to the details of the contraction from start to finish.

The electrical currents employed in stimulating muscles to contraction are of two kinds—the galvanic or constant current, and the induced or interrupted current.

The *galvanic current* is conveniently supplied by a Daniell's cell, (E, Fig. 113), in which zinc is the positive and copper the negative element. These metals are connected with wires to the poles or electrodes. The electrode attached to the zinc element is not, however, the positive, but the negative, or *kathode*, pole, and, similarly, the electrode attached to the copper is the positive, or

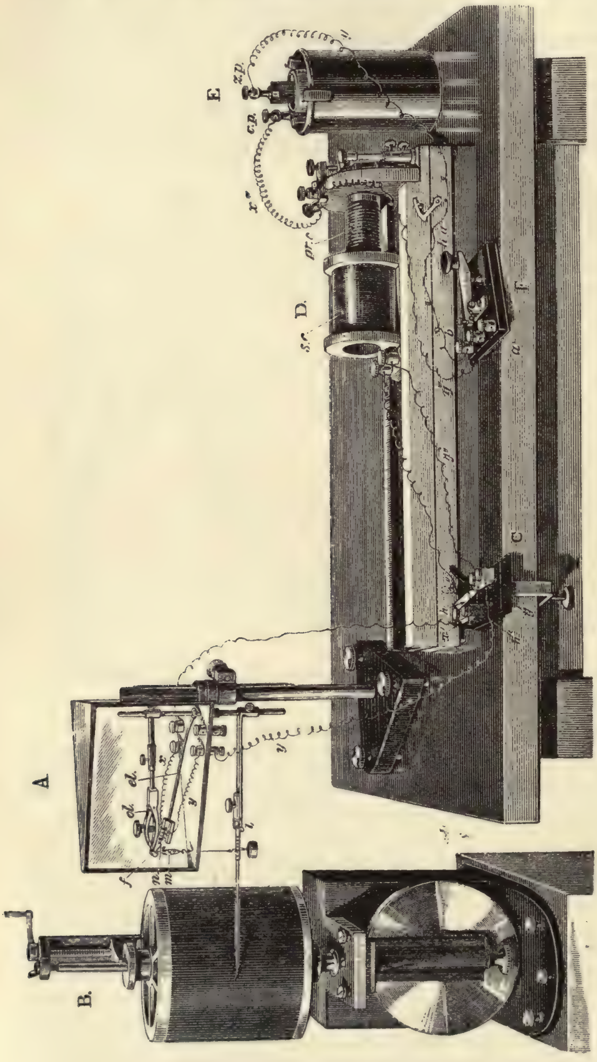

Fig. 113.—Diagram showing a Typical Arrangement of Apparatus and Instruments for Experiments with a Muscle-Nerve Preparation (Foster).

A, The moist chamber; *m*, muscle; *n*, nerve; *f*, femur; *cl*, clamp. The nerve is shown laid over the end of the electrode-holder *el*, connected by the wires *x y* to the outside of the chamber; *l*, the lever with which the muscle is connected by a thread and S-hooks; B, Rotating drum, carrying the smoked paper on which the lever makes its tracing; C, a key for controlling the connection of the electrodes in the moist chamber with the secondary circuit *s c* of the induction-coil D; F, a key for making or breaking the connection of the battery-cell E with *pr c*, the primary circuit of the induction-coil D.

anode, pole. Within the battery the current flows from zinc to copper, outside the battery—viz., between the poles, it flows from copper to zinc. The circuit is completed by bringing the poles together, known as ' making '; it is broken by separating the poles, known as ' breaking.' When this current is passed through a galvanometer—an instrument which detects the existence, direction, and intensity of currents—it flows through this apparatus from the positive to the negative pole. So much confusion results from the use of the terms ' positive ' and ' negative '—which, as we have seen, have two opposite meanings, depending upon whether the current is passing through the battery or through the poles—that Waller has proposed that physiologists should call the copper ' galvanometrically positive,' and the zinc ' galvanometrically negative,' in the same way that physicists employ the terms ' electro-positive ' and ' electro-negative ' to indicate the positive and negative elements respectively.

The *induced* or *interrupted current* is produced by passing a galvanic current through an induction-coil (D, Fig. 113). This consists of a primary coil, *pr c*, connected with the Daniell's cell, E, and a secondary coil, *sc* D, capable of a sliding adjustment near to or away from the primary coil. The nearer the coils are together, the stronger the current. To the secondary coil wires are attached conveying the induced current. Between the battery and the primary coil is introduced an appliance for making or breaking the current. This may be done by hand, when single shocks are required, by means of the key F, Fig. 113, or automatically by means of an interrupter, when a rapid succession of make and break shocks are required. This may be seen in Fig. 113, to the right of the standard supporting the primary coil.

If a suitable muscle preparation be connected with a galvanic battery and a *weak* constant current passed through it, at the moment of ' making ' the muscle gives a twitch, and nothing more occurs to the eye, though the current continues to pass. If the current be made stronger a twitch occurs both at ' make ' and ' break,' and if the current be sufficiently powerful it will be observed that the contraction at ' make ' is more vigorous than that occurring at ' break.' This reaction takes place more obviously with striated than with plain muscle. The contraction which occurs at ' make ' starts from the negative pole, and is known as the *closing contraction ;* that which occurs when the current is broken starts at the positive pole, and is known as the *opening contraction*. This is described as ' the laws of polar stimulation.'

When a muscle-nerve preparation is stimulated by a single *induction* shock the contraction which occurs at ' break ' is stronger than that taking place at ' make.' This appears to be an opposite condition to the effect produced by a *constant* current ; as a matter of fact, it is not, but is due to an ' extra current ' developed in the primary coil, which, being in the opposite direction to the battery current, renders the ' make ' stimulus ineffective.

The efficiency of an electric current depends upon the rate of variation; the tissues are immediately excited by a sudden increase or sudden diminution of a current, though they may be unresponsive when the current is gradually increased even to a considerable strength. The resistance of animal tissues generally to electrical currents is very considerable; the body is a bad conductor.

Induced currents stimulate muscle less readily than nerve. When a nerve has degenerated induced currents produce no contraction of the muscle, while continuous currents are capable of stimulating it into contracting activity.

The most conveniently controllable stimulus for experimental purposes is that obtained as single induction currents or the interrupted current of an induction-coil. These have the advantage of being extremely efficient as stimuli, and of giving rise in the nerve to impulses which we may regard as the nearest artificial approach to the impulses which in the body are discharged along the nerves by the cells of the central nervous system.

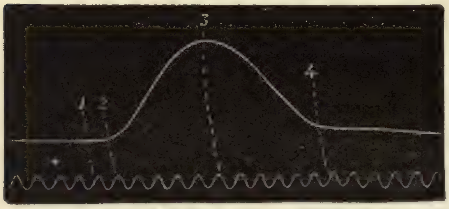

Fig. 114.—The Curve from a Single Contraction of the Gastrocnemius Muscle of the Frog (Waller).

From 1 to 2 is the latent period; from 2 to 3 the period of shortening; from 3 to 4 the period of relaxation. The sinuous line below the curve indicates periods of $\frac{1}{100}$ second.

When a muscle is stimulated to contract, it becomes shorter and thicker, but there is no change in volume. If made by means of a myograph (Fig. 113) to trace its contraction on a revolving drum, a muscle curve is produced. A **muscle curve** consists of three parts: (1) A period following stimulation during which no contraction occurs; it is known as the *latent period*, and during this time the muscle is preparing itself for work; (2) a period of *contraction* or shortening; (3) a period of *relaxation*.

The length of time involved in the various phases of a contraction may be measured by bringing a time-recorder, vibrating fractions of a second, to bear on the smoked surface of the revolving drum; the sinuous line in Fig. 114 below the muscle curve is produced in this way. Though the nerve was stimulated at the point marked 1 on the tracing, it was not until 2 was reached that the muscle responded, the time value for the latent period being $\frac{1}{100}$ second. As a matter of fact, the latent period is less than this, for a minute loss in time occurs in the impulse passing along the nerve, and there are also instrumental defects, such as friction of the lever. When these are deducted the latent period is reduced to about $\frac{1}{250}$ second. The entire contraction from the instant of stimulation to the end of relaxation occupies about $\frac{1}{10}$ second.

The latent period, contraction, and relaxation of a muscle are affected by certain conditions. It is found that *with an increase in the weight* a muscle may be called upon to lift, the less the contraction while the latent period is prolonged. By continuing to weight the muscle a point is reached when it is unable to lift the load. With an *increase in the strength of the stimulus* there is, up to a certain point, increased contraction, and also a shorter latent period ; beyond this point, known as a 'maximal stimulus,' an increased stimulus produces no effect. It will be remembered that this is very different from the effect of stimulation on heart muscle (p. 50), the weakest or minimal stimulus applied to cardiac muscle producing a maximal contraction. If a muscle is kept contracting and recording its movements, it is easy to observe that as it settles down to its work the contractions improve, each being higher than the preceding. This is known as the *beneficial effects of contraction*, and the character of the tracing recorded is described as a 'staircase' (see Fig. 115). If the contractions be maintained sufficiently long the muscle becomes fatigued. Under the influence of fatigue the period of contraction, and especially of relaxation, becomes longer (see Fig. 116) in which the muscle has been made to contract at the same point at each revolution of the drum. If the muscle be left to itself it will recover, though on restimulation it is more easily fatigued than before.

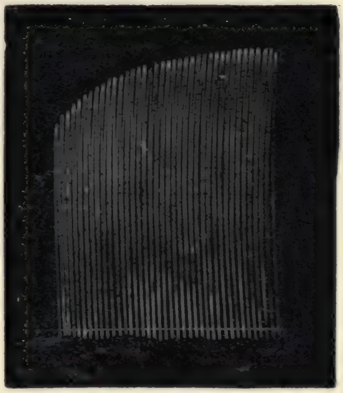

FIG. 115.—'STAIRCASE,' SKELETAL MUSCLE : FROG (STEWART).

The *effect of warming* a muscle is to shorten the latent period and quicken the contraction. The results obtained are not, however, so simple as would appear from this statement ; there are two maximal temperatures at which the frog's muscle does its best work—viz., at about 7° C. and about 28° C. (45° F. and 82° F.). There are two temperatures at which the muscle loses its irritability—viz., 0° C. and 37° C. (32° F. and 98° F.). *Cold* prolongs the latent period and also the period of contraction, but heightens the excitability. When the temperature of muscle is raised beyond a certain point *heat rigor* occurs (see p. 418).

The *effect of veratrine poisoning*, on muscular contraction, is very remarkable ; apart from the fact that the curve sometimes shows a second contraction, there is a prolonged period of retarded relaxation or maintained contraction (see Fig. 117).

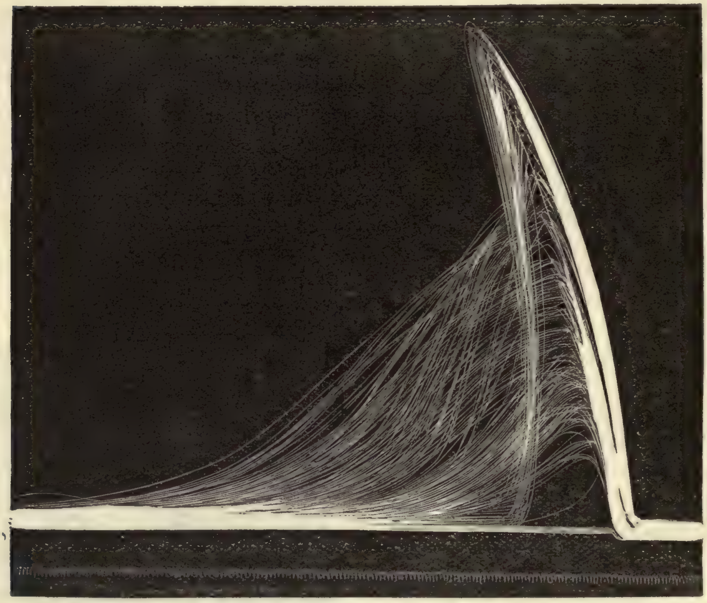

FIG. 116.—FATIGUE CURVE OF SKELETAL MUSCLE ; GASTROCNEMIUS OF FROG (STEWART).

Time-tracing $\frac{1}{100}$ of a second. The curve is read from right to left.

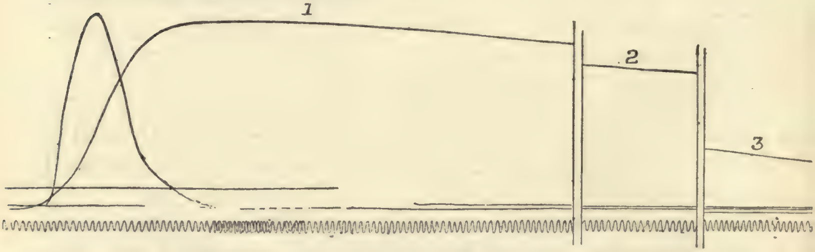

FIG. 117.—VERATRINE CURVE COMPARED WITH NORMAL : FROG'S GASTROCNEMIUS (STEWART).

The tuning-fork marks hundredths of a second. Between 1 and 2 a portion of the time-tracing corresponding to one and a half seconds has been cut out, and between 2 and 3 a portion corresponding to one second. The Veratrine curve does not show a peak. At 3 it has not yet fallen to the base-line.

This retarded relaxation is termed **contracture** ; it may be produced in other ways—viz., by repeated electrical stimulation of a muscle. The muscle, while being held in a state of maintained contraction, is undergoing quick contractions and relaxations. It has been supposed that such a condition may not be unfavourable to a muscle at the beginning of work, though unfavourable when the muscle begins to tire. It is very likely that the condition of muscular cramp may be associated with this state of a muscle, and that it represents the bulk of the cases of so-called dislocation of the patella in the horse.

Muscle Wave.—When the impulse enters a muscle at the middle of each fibre, the part nearest the end-plate contracts first, and the impulse spreads each way to the end of the fibre ; this process is so rapid, the fibre only being, as we have seen, about 1 inch in length, that for all practical purposes the whole muscle contracts at one and the same time. When, however, the nerve-endings in a muscle are paralysed by curare, the part becomes at once practically nerveless, and if under these conditions *one end* of the muscle be stimulated, a wave of contraction passes along it to the other at a rate of about 3 to 4 metres (10 or 12 feet) a second in the curarised muscle of the cold-blooded frog. In the muscles of warm-blooded man, where the metabolic processes are more active than in the frog, the rate of propagation is greater, and may be taken as 10 to 13 metres (30 to 40 feet) per second. The time which the wave takes to pass any *one* point of the muscle is extremely short, $\frac{1}{10}$ second ; and if (in frog's muscle) we take its velocity as at least 10 feet per second, a simple calculation shows that the *length* of the wave is about 1 foot (35 centimetres). This is a fact of great interest in connection with the efficiency of a muscle as a machine. It ensures that each single fibre of which the skeletal muscles are composed, and hence the whole muscle itself, can be placed in a state of complete contraction from end to end at the same moment. The skeletal muscles when exposed immediately after death show irregular contractions, bundles of muscle fibre contracting and relaxing irregularly, producing a flickering, quivering appearance. This is known as *fibrillar contraction*, and, as we have already seen, it becomes a serious pathological condition when it affects the heart muscle.

Summation.—If instead of passing a single stimulus into a muscle-nerve preparation, two are sent in, so arranged that the second follows the first before the muscle has time to relax from the first contraction, the contraction due to the second stimulus is superposed on the first, and the effect obtained is a stronger total contraction. If a third stimulus be sent in before relaxation occurs from the second, the lever of the muscle preparation will describe a curve still higher than the preceding, and so on, until a maximum is reached when it can go no higher. Such a piling up of contraction on contraction is known as *summation of contractions* (Fig. 118). It will be remembered that one characteristic of heart muscle is the absence of summation ; the fibres of the heart yield their best possible contraction to a single stimulus, be it weak or strong, single or multiple.

Tetanus.—If an induction current be applied to a muscle or its nerve, a rapid succession of stimuli is thus introduced, and there is no time for complete relaxation to occur between each successive stimulus. This may be seen in the lower curve of Fig. 119, in which ten stimuli per second were passed into the muscle, and partial relaxation only will be observed to have occurred between each of them. In the middle curve twenty stimuli per second were used, and the amount of relaxation is represented by a slightly wavy line ; in the upper curve thirty stimuli per second were employed, and the curve shows no relaxation ; the muscle is in the condition of electrical *tetanus*, and tetanus, therefore, consists of the summation of a series of short contractions with an insufficient interval for intervening relaxation.* The number of stimuli per second required to provoke tetanus depends on the condition of the muscle, the nature of the muscle, and the class of animal ; for example :

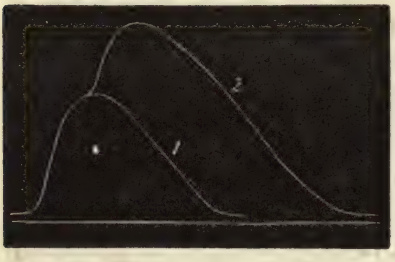

FIG. 118.—SUPERPOSITION OF CONTRACTIONS (STEWART).

1 is the curve of contraction due to the first stimulation ; 2 is the curve of the second contraction, superadded to 1 by applying the second stimulus at the moment when the first contraction had nearly reached its maximum.

In the bird, 100 stimuli per second.
In man, 40 stimuli per second.
In the rabbit, 20 to 40 stimuli per second for the pale voluntary muscles.
In the rabbit, 10 to 20 stimuli per second for the red voluntary muscles.

In insects, whose muscles can contract a million times an hour, 300 stimuli per second are required to produce tetanus. A fatigued muscle is more readily tetanised than one which is fresh ; unstriped muscle requires less frequent stimulation than striped.

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* The tetanus of the physiologist must not be confused with the tetanus of the pathologist ; the latter is a bacterial affection producing a poison which causes spasm of many of the voluntary muscles of the body especially of the limbs and jaw.

All the ordinary voluntary muscular contractions of the body have usually been regarded as tetanic in nature—viz., as a series resulting from a succession of impulses passed into the muscle so rapidly that there is no interval for relaxation. Other investigations have supported the view that in all probability a voluntary contraction is a prolonged single contraction, caused by one long constant stimulus. On the other hand, it has been urged, on the basis of experiments made by stimulating the motor areas of the cerebral cortex with stimuli of varying frequency, that a motor cell cannot discharge a single impulse ; it must be a series, and the normal rate in man under the influence of the will is ten per second. Until recently the chief evidence in favour of an ordinary voluntary contraction being tetanic was that supplied by the musical note furnished by a contracting muscle. This note Helmholtz considered corresponded to twenty vibrations per second. The electrical oscillations of the string galvanometer support the view that the shortest possible voluntary contractions are tetanic in character.

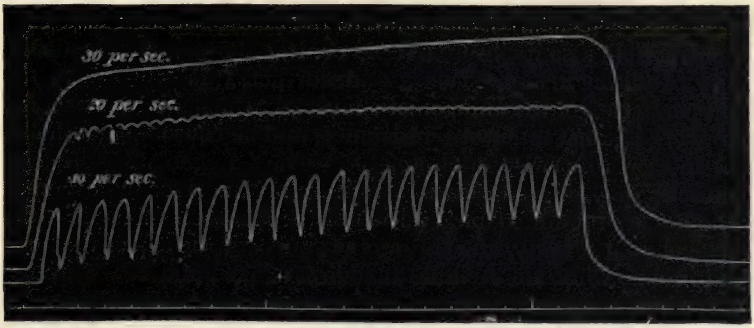

FIG. 119.—SUMMATION CURVES OF MUSCLE CONTRACTION (WALLER).

The lower curve is one obtained by stimulating the muscle ten times every second ; the intervals of relaxation are clearly seen, though there is a slight summation shown by the slanting rise of the tracing. In the middle curve the shocks were twenty per second, and the relaxation is only of a very partial kind. The upper curve is that of tetanus.

Elasticity and Extensibility.—Elasticity is the property a body possesses of returning to its shape after stretching ; extensibility is the power a material possesses of stretching. A piece of steel is elastic, a piece of putty is extensible. If a steel spring or a piece of elastic be tested by loading them with weights, the stretching is proportional to the weight employed ; but if muscle be gradually weighted, it is found that the greatest degree of extension occurs at the beginning, and as the load is increased the extensibility becomes less. A living muscle is very extensible, but its elasticity, though perfect, is slight. It is therefore stretched by a slight force, and returns to its original length when the extending power is removed. A contracted muscle is more extensible than one which is uncontracted; this is a protective mechanism intended to prevent rupture of the fibres during powerful muscular effort, and is capable of ready proof clinically. A ruptured muscle is incomparably less frequent than a ruptured tendon.

Tone.—In the body the muscles, as we pointed out previously, are always in a condition of *elastic tension*—viz., they are not slack, flabby masses, but slightly on the stretch, as may be demonstrated by the gaping which occurs when they are divided. The use of this elastic tension is to stimulate the changes which lead to a contraction, also to ensure a rapid contraction without the necessity of taking in any 'slack'; and, further, it is essential to the proper action of the antagonistic muscles, which are thus enabled to work against an elastic resistance, and so cause a smoothness of motion otherwise unobtainable. The antagonistic action of muscles may be well seen in a rupture of the flexor metatarsi of the horse; the unbalanced action of the gastrocnemius jerks the leg behind the body, and throws the skin over the cap of the hock into folds, while the Achilles tendon is kinked and bent through slackness. The elastic tension of muscle is not only a valuable stimulus to contraction in all varieties of muscle, but is also of the greatest value in diminishing shock and strain; nowhere is this better seen than in the heart and bloodvessels. Tone is the term also applied to that slightly contracted condition of skeletal muscles associated with posture, which leads to the upright condition of the body being maintained. It is due to the continuous discharge of reflex impulses from the spinal cord to the muscles. In the normal posture of animals it is the extensor muscles of the limb which maintain the upright attitude, and, in the case of the horse, who may have to stand for weeks, the extensors are severely tried.

Work of Muscle.—If a muscle preparation is loaded with successively greater weights, it is found that up to a certain maximum the load absolutely increases the amount of work done by the muscles. This is considered to be due to the influence of the *tension* exercised on the fibres, the muscle adapting itself to circumstances and meeting the increased weight by an increased effort, as we have already seen in the case of the heart muscle. By continuing to increase the weight the muscle preparation becomes overloaded, and in consequence shortens less. These facts are illustrated in the following table:

Load in Grammes.	Lift in Millimetres.	Work done in Gramme-Millimetres—viz., the Load Multiplied by the Height.
5	27·60	138·00
15	25·10	376·50
25	11·45	286·25
35	6·30	220·50

This table also shows that when the muscle shortened the least it lifted its greatest weight. It is obvious that if a muscle lifts no weight it does no work, and its energy goes off as heat. Experience and experimental observation show that there is a load, which differs in various animals of the same species, depending upon the *quality** of their muscles, from which the greatest proportion of effective work can be obtained. Finally there is a load just in excess of the strength of the muscle known as *the absolute power of the muscle.* This latter has led to a paradox associated with the name of Weber—viz., that a contracting muscle may have the same length as one uncontracted. Yet we are all familiar with the fact that this is so ; a horse called upon to draw a greater weight than he can move is employing strongly contracting muscles, but they become no shorter. The absolute power of a muscle, according to Weber, varies with the cross area. Measured by this standard the muscles of one animal may be far more effective machines than those of another, and probably the muscles of insects are superior to those of vertebrates.

If the weight of the load and the height to which it is lifted be known, the work done by a muscle is readily calculable. Work equals the load lifted multiplied by the height through which it is raised, and may be expressed as pounds or tons lifted 1 foot or grammes or kilogrammes lifted 1 metre.†

The **ergograph** is an instrument employed for recording voluntary muscular contraction in man ; it is shown in Fig. 120. The person experimented upon lifts a known weight to a definite height, which is recorded on a drum. Each contraction is followed by the same interval of rest. Observations with this instrument show that after complete fatigue at least two hours are required for the muscle to recover sufficiently to repeat its first record. If, instead of resting the completely fatigued muscle, further muscular effort is made, the period required by the muscle for recovering is greatly prolonged. This is in accordance with practical experience. The ergograph emphasises the ill-effects of straining the tired machine. The effect of hunger, want of rest, mental activity, is found to diminish the amount of work produced. When the circulation in the muscle is improved by massage, more work is produced. The effect of improving its nutrition by food, especially by a readily soluble and easily absorbed substance such as sugar, is said to increase quickly its power of performing work. Finally, the effect of making a prolonged call for work upon one group of muscles is to diminish the activity of the others. The results obtained by the ergograph are those which accord with experience, but it is unfortunate that the personal element cannot be excluded from the experiments, especially where the questions of food and work are concerned.

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* Robertson points out that in the race-horse the difference between a 'stayer' and a 'non-stayer' lies in the relative proportion which the pale bear to the dark red fibres in muscle. In the stayer the dark red fibres greatly predominate. ('The Principles of Heredity Applied to the Race-Horse,' J. B. Robertson, M.R.C.V.S.)

† A 'horse-power,' the unit used in engineering, equals 33,000 foot-pounds of work *per minute.*

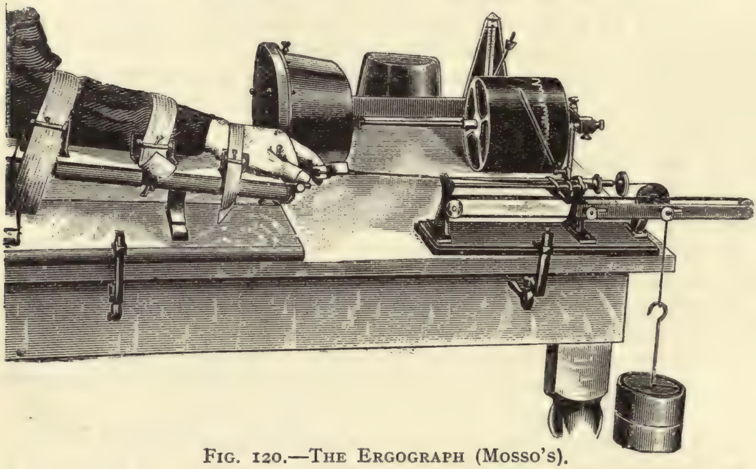

FIG. 120.—THE ERGOGRAPH (MOSSO'S).

In connection with the work done by muscle, it is interesting to institute a comparison between the work yielded by the animal body and that by a well-constructed machine. The best triple-expansion engine may yield as work some 10 to 15 per cent. of the available energy in the fuel, the balance is lost as heat; in other words, the 'efficiency'—that is, the fraction of the heat it receives which it converts into work—of a good engine is $\frac{1}{10}$ to $\frac{1}{7}$. In the animal body various statements have been made as to the proportion of work done to the available energy. Chauveau, working with the lip-muscle of the horse, placed the work at 12 to 15 per cent. of the energy liberated, the difference being accounted for as heat. If this were the case the muscle machine would seem to be very little more economical than the steam-engine. Now, Fick showed, some thirty years ago, that the efficiency of an *excised* muscle of the cold-blooded frog may be as much as $\frac{1}{4}$ or even $\frac{1}{3}$, and we may not unreasonably expect that mammalian muscle, in the body with its circulation intact, would be still more efficient. And this is borne out by Zuntz's experiments on the dog. He calculated that one-third of the energy liberated appeared as work, while by experiments on men it was found that the proportion was 25 per cent. as external work for the muscles of the arms (turning a wheel), and 35 to 40 per cent. for the legs (in mountaineering), from which it would appear that the muscles of locomotion are superior as work producers. Experiments carried out on the horse by Zuntz* show that 34·6 per cent. of the total energy contained in the food were converted into muscular work. This shows that the animal body possesses an efficiency of one-third in the case of the horse, and somewhat higher than this in man, which far surpasses the best heat-engine.

Interesting as the comparison may be, a word of caution is necessary. It is true that an engine and a muscle each take in energy and utilise a part of it to do external work, but they work in different ways and along different lines to produce the same results. Thus the steam-engine receives its energy as heat, originated by the combustion of fuel in the boiler-furnace, converts a varying fraction of this into work, and discharges the remainder, degraded in temperature, but otherwise unaltered. A muscle, on the other hand, receives its energy in the form of the food it takes from the blood. This it metabolises by chemical processes, which are ultimately oxidational, converting the potential energy of the food partly into work and, unlike the engine, partly into heat (see p. 411), and giving off degraded products of its metabolism, of which one is the same as that from the furnace of an engine—viz., carbon dioxide. These few remarks must suffice to emphasise the fact that a muscle is a *chemical-engine*, and not a heat-engine. As Fick was careful to point out, if an attempt is made to explain the working of a muscle on the thermodynamic principles which govern the working of a heat-engine, one is landed in the absurd result that a muscle only converts into work $\frac{1}{100}$ part of the potential energy it receives, the remaining $\frac{99}{100}$ necessarily being converted into heat ; we have seen that the efficiency of a muscle may be $\frac{1}{3}$. In the case of insects, with their astounding locomotive activities, if the efficiency of their muscles could be determined it would probably be found to exceed that of mammalian muscle.

Muscle Currents.—Great controversy has taken place as to whether currents of electricity exist naturally in uninjured muscle. It is found, for instance, that a piece of muscle isolated from the body, and placed in connection with a galvanometer, may be made to demonstrate the presence of electric currents which behave in a perfectly regular manner in passing from one definite point on the muscle to another. These are the so-called natural *muscle currents*, or **currents of rest**; they are found to pass in a certain direction—viz., from the longitudinal surface of the muscle to the cut extremity. The natural surface of the muscle, therefore, corresponds to the copper of a Daniell's cell, the cut ends to the zinc element; the surface of the muscle is in consequence galvanometrically positive, the cut ends galvanometrically negative (see p. 395). The more the ends are injured the more galvanometrically negative they become. It is now known that the *currents of rest* in muscle are caused by the *injury* inflicted on the muscle in its course of preparation for the experiment. They are in consequence frequently described as **injury currents.** Muscle at rest and absolutely uninjured gives *no current whatever.*

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* 'Metabolism of Nutrients in the Animal Body and the Source of Muscular Energy,' United States Department of Agriculture, vol. vii., No. 7, 1895.

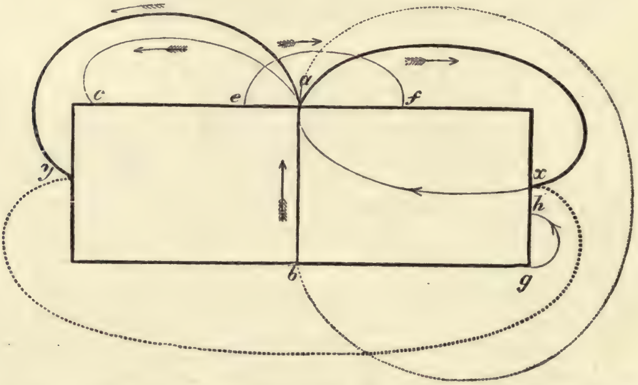

FIG. 121.—DIAGRAM ILLUSTRATING THE SO-CALLED ELECTRIC CURRENTS OF REST (INJURY CURRENTS) OF MUSCLE AND NERVE (FOSTER).

Being purely diagrammatic, it may serve either for a piece of muscle or nerve, excepting that the currents at the transverse section cannot be shown in a nerve. The arrows show the direction of the current through the galvanometer.

a, *b*, The equator. The strongest currents are those shown by the dark lines, as from *a* at the equator to *x* or to *y* at the cut ends. The current from *a* to *c* is weaker than from *a* to *y*, though both, as shown by the arrows, take the same direction. A current is shown from *e*, which is near the equator, to *f*, which is farther from the equator. The current (in muscle) from a point in the circumference to a point nearer the centre of the transverse section is shown at *g*, *h*. From *a* to *b*, or from *x* to *y*, there is no current, as indicated by the dotted lines.

If while the galvanometer is registering the direction of an injury current the muscle preparation be stimulated with an interrupted current, a backward swing of the needle of the instrument towards zero indicates that the injury current is diminished; this diminution is termed the **negative variation.**

If an *uninjured* muscle, which is giving no currents, be stimulated by means of an interrupted current into contracting activity, it exhibits electrical phenomena, called the **current of action.** It is the production of this current which accounts for the negative variation of the injury current. The action current is of such a nature as to give rise to what is known as a *diphasic* variation in the current of a muscle, as shown by the needle of the recording galvanometer swinging first one way and then in the opposite direction. The double variation is due to the fact that the point on the muscle to which the stimulus is applied becomes negative to all points of the muscle at which the wave of contraction, resulting from the stimulation, has not yet arrived. This negativity occurs during the 'latent period' (p. 396), and passes along the muscles as a wave which precedes, or in some cases accompanies, the wave of contraction. Thus if, as in Fig. 122, a muscle be stimulated at *a*, while the points *b* and *c* are connected through a very sensitive galvanometer, at the moment of stimulation *a* becomes negative to the rest of the muscle. As this negativity sweeps along the muscle it passes first over the point *b*, which thus becomes negative to *c*, and the current in consequence flows from *c* to *b* through the galvanometer. Midway between *b* and *c* is a neutral point, as shown by the fact that no current is passing through the galvanometer. Immediately afterwards the current passes over the point *c*, and *c* then becomes negative to *b*, as shown by the current flowing through the galvanometer in the opposite direction. Every contraction of a muscle gives rise to a diphasic variation, which passes along the muscle either in advance of or accompanying the contraction wave. These phenomena, while of the greatest interest in the case of muscle, become still more important in the case of a nerve, since they provide the only accurate means of following the passage of an impulse along a

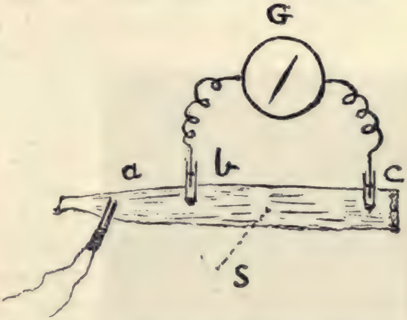

FIG. 122.—SARTORIUS MUSCLE ARRANGED TO DEMONSTRATE THE DIPHASIC VARIATION OF ACTION CURRENT IN MUSCLE (OR NERVE).

S, Sartorius; *a*, stimulating electrodes; *b*, *c*, non-polarisable electrodes as 'leads' to *G*, the galvanometer. The electrode *c* is intentionally not placed on the injured end of the muscle as it would be for demonstrating more 'negative variation,' since the strong negativity of the injured end would mask the desired phenomenon. A similar arrangement suffices to demonstrate the same phenomenon in a piece of nerve.

piece of *isolated* nerve, which does not, as does a muscle, change its shape or exhibit other obvious changes when stimulated.

The electrical change in muscle can be observed without the assistance of any apparatus, by means of an experiment as old as electricity itself. In the hands of Galvani, it was described as electricity without metals. The nerve of a nerve-muscle preparation (M, Fig. 123) is brought into contact with another muscle, M′, in such a way as to touch at two points—viz., the cut end and the surface of the muscle. The current of injury in the latter travels along the nerve, and produces a contraction in M. With the same preparation it can also be shown that if M′ be stimulated at S and made to contract, the negative variation which accompanies the contraction of M′ will produce a contraction of M. This is known as a 'secondary contraction,' while the above preparation is spoken of as the *rheoscopic frog*.

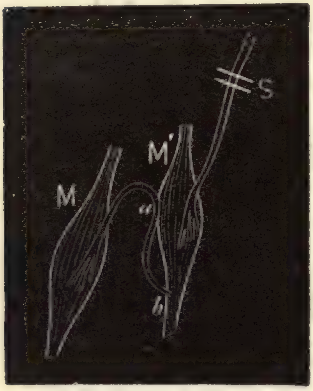

FIG. 123.—SECONDARY CONTRACTION.

The electrical phenomena in muscle are not an isolated example of electric currents in the body. Closely similar phenomena are demonstrable in nerves, which we shall shortly study, and electrical changes accompanying their functional activity occur in secreting glands, in the eye, and to the highest degree in the electrical organs of certain fish. These electrical organs are modified muscle or skin glands.

The Changes in Active and Resting Muscles. — The physiological changes occurring in muscles are remarkably active. The processes which result in muscular contractions use up at every moment the combustible material of their structure, and the products arising from their metabolism have to be got rid of at once and repair brought about. Changes are also constantly occurring even during the period of muscle rest. Muscle activity is characterised by muscle waste, muscle rest is characterised by a preponderance of the process of repair; we must therefore learn the nature of the waste and repair occurring in muscles.

The oxygen carried to resting muscles by the blood is absorbed in considerable quantities, and a volume of carbon dioxide, in slightly less quantity than corresponds to the oxygen absorbed, is returned to the venous blood. Whether a muscle is at rest or active, it is always absorbing and storing up oxygen, and giving off carbon dioxide. The absolute amount of these varies; during work the oxygen used up and carbon dioxide produced are both increased, and the increase provides some measure of the work performed. Even during rest a muscle is doing work, for we have learnt that it is always in a condition of *tonus*—viz., of slight contraction. Since a muscular contraction is essentially the outcome of an oxidational process, the storage of oxygen by the resting muscle may be said, in Pflüger's words, ' to wind it up ' in preparation for its contracting activity. This accounts for the fact that an excised muscle of the cold-blooded frog can be made to give some hundred contractions when suitably treated. In mammalian muscle, on the other hand, with its much greater metabolic activity, this quiescent storage of oxygen does not suffice to maintain its irritability for more than the briefest interval after its blood supply is cut off.

In an active muscle the bloodvessels are more dilated than in the muscle at rest, and this dilatation provides for the increased quantity of blood now required by the part. By means of the blood the irritability of the muscle, or its power of contraction, is maintained ; whatever leads to a smaller quantity of blood being sent to an active muscle produces partial or complete paralysis of the group or groups of muscles affected. This is well seen in the horse when suffering from thrombosis of the iliac arteries ; the blood supply is sufficient during the time the animal is at rest, or even at a walk, but if called upon to trot muscular cramps occur, followed by paralysis.

The study of metabolism has prepared us for the statement that the chemical changes occurring during contraction do not normally affect the nitrogenous elements of the muscle. There is probably no increased output of nitrogenous substances such as kreatin. The excretion of any increased amount of urea is variable, irregular, may even be non-existent, and is in no case remotely proportional to the work done. This is true as long as the body is supplied with a sufficiency of the non-nitrogenous carbohydrates and fats. If they are deficient, then increased muscular activity does lead to an increased formation of urea, since the muscle now has to metabolise its proteins to provide the energy necessary for the work performed and the heat simultaneously produced. The main products of muscular waste are therefore to be looked for in the destruction of stored-up carbohydrate material.

Carbohydrates and fats are normally the chief source of muscular contraction. The carbohydrates are represented by glycogen, formed, as we have seen, by the sugar brought to the muscle, and by dextrose. A well-nourished muscle contains 0·5 to 0·9 per cent. of its weight as glycogen. This local store of animal starch is, under the influence of an enzyme, converted back to sugar, and in this form is capable of being converted into energy under the influence of oxidising enzymes; as we have previously seen, the contraction of muscle leads to the disappearance of glycogen. In this condition, though free from glycogen, the muscle still continues to contract, and if the view be adopted that sugar is the source of muscular energy, there is still sufficient for the purpose existing in the blood, which even under starvation continues to maintain its normal 0·1 per cent. Under starvation this sugar is furnished by the breaking down of body protein, but under the ordinary condition of nutrition, when work has emptied the muscles of glycogen, there is ample sugar available from the store of carbohydrate taken into the body. Many circumstances seem to point to sugar as being necessary to the chemical changes occurring during contraction. Quantitative investigations on the muscular work performed by man, as measured by the ergograph, has, it is said, shown that sugar increases the amount of muscular work which can be performed, yet it has never been proved that sugar is an essential food for muscular activity. Unfortunately, the suggestion of its utility has, in the hands of ignorant laymen, frequently led to deplorable errors in the dieting of working-horses.

The changes occurring in muscles as the results of contraction may be tabulated as follows:

1. More oxygen is consumed.
2. More carbon dioxide is produced.
3. Glycogen is used up.
4. Lactic acid is formed.
5. Heat is produced.

The first three we have already studied. The formation of acid in muscle as the result of contraction has given rise to a good deal of inquiry, and very different results have been obtained. Lactic acid is found in muscle; it is not, as we have seen, the ordinary lactic acid found in milk, but a form optically active to which the name 'sarcolactic acid' has been given. It appears clear that resting muscle only contains a trace of lactic acid (0·03 per cent.), while under the influence of contraction a marked amount is present (0·22 per cent.), and rigor, whether produced artificially by heating the muscle or naturally after death, leads to the production of as much as 0·3 to 0·5 per cent. The source of the acid is not agreed upon by physiologists; some regard it as a product of protein metabolism, others as an intermediate product formed from sugar.

During muscular activity heat is produced; the blood returning from a muscle has a higher temperature than that going to it. Colin found the temperature of the masseter muscle of the horse to rise 5° F. through feeding. The whole body temperature is raised during work, especially in the horse, and does not fall for some time after. In dogs also a rise of temperature of several degrees may be obtained by stimulating the spinal cord and thus producing muscular contractions. A contracting muscle liberates energy in the form of both work and heat. We have seen reasons for regarding the oxidation of the non-nitrogenous carbohydrates as the normal source of this energy, and have referred to the quiescent storage of oxygen during rest as accounting for the prolonged possible activity of an isolated frog's muscle. In connection with this it is not uninteresting to calculate, as Fick has done, the amount of carbohydrate necessarily oxidised to provide all the energy as work + heat furnished by a single maximally vigorous contraction of a frog's muscle. Knowing the heat of combustion of, say, glycogen, and converting the work of the muscle into heat by Joule's equivalent, we find that 1 gramme of frog's muscle can provide all the energy it sets free in a single maximal contraction by the oxidation of 0·0006 milligramme of carbohydrate. In the case of fat the necessary amount would be still less—viz., 0·00025 milligramme. This may serve to diminish our surprise at the working activity of which an excised muscle is capable.

Causation of a Muscular Contraction.—This is a problem as yet unsolved; our previous studies in every way point to the oxidation of carbohydrate substance as being the source of energy, and we have seen that it is impossible for a muscle to contract without using up oxygen and producing carbon dioxide. But we are now brought face to face with a paradoxical condition; if muscle be exposed to the vacuum of a gas-pump no free oxygen can be obtained from it, while if the ordinary nerve-muscle preparation be taken and placed in a jar of hydrogen it continues to contract, and, even still more remarkable, it continues to produce CO_2 though no oxygen exists in the atmosphere surrounding it. As CO_2 cannot be formed without oxygen, it is evident the oxygen must come out of the muscle, and to meet this difficulty it is supposed that the muscle molecules store up oxygen during rest in a hypothetical compound of hydrogen and carbon, to which the name *inogen* has been given; during muscular contraction this compound breaks down, and the waste products are liberated.

Statements such as these help very little to a better understanding of the cause of a muscular contraction. No one doubts the process being at bottom chemical in its nature, large and complex molecules being reduced to smaller and simpler ones, but how this can lead to contraction of a muscle is still unexplained. An impulse is conveyed to a muscle by means of a motor nerve, and through the medium of an end-plate it becomes the stimulus which fires off an explosive compound in the muscle substance, resulting in a contraction and the production of work and heat. Such a statement is obviously a mere skeleton, and takes us little nearer to an understanding of what really constitutes a muscular contraction.

Fatigue.—The influence of fatigue on muscular contraction has previously been dealt with. The cause of fatigue is the using up of the contractile substance of the fibres, and the accumulation in the muscle of the chemical products of contraction. In fact, if a fatigued muscle be washed out with normal saline solution and a little weak alkali circulated through its bloodvessels, it becomes restored, and regains its power of contraction. A muscle at work *in* the body is protected from ready fatigue by the ever-circulating blood, which supplies it with food and carries off the waste products of its activity.

The material in muscles which gives rise to fatigue is probably sarcolactic acid, and by passing a solution of this acid into muscles the typical phenomena of muscle fatigue may be artificially induced. The production of potassium salts may also be a cause of fatigue, in spite of the fact that they are usually found in muscle, yet potassium salts in their action on this tissue rapidly destroy its irritability.

Attention has been drawn to the fact (p. 390) that muscles are connected by elaborated nerve-endings with sensory nerves, to whose existence the so-called ' muscular sense ' is due. It is therefore conceivably possible that the sensation of general fatigue which arises from excessive muscular exertion is due to a cerebral appreciation of the changes brought about in the muscles as the result of their contracting activity, and may be looked upon as a protective mechanism against straining the machine. On the other hand, muscular activity implies the action of central nerve-cells in which the impulses which give rise to the contractions of the muscles are originated, of the passage of these impulses along the motor nerves, and of their communication to the contractile fibres by the agency of the end-plates. Hence the phenomena of fatigue, if we regard it as a ' weariness ' of the body as a machine, may be really due to a fatigue of the central cells, of the motor nerves, or of the end-plates. We may at once dismiss the motor nerves from our consideration, inasmuch as nerves do not appear to be capable of fatigue. Now, the blood of a fatigued animal contains fatigue products, and if it be transferred into the circulation of a normal animal, all the symptoms of fatigue are produced. If the spinal cord be divided and the distal end stimulated, the hurried respiration of fatigue may be produced as the result of muscular contractions (see p. 142). Possibly, therefore, the phenomena are due to the injurious action of the products of muscular activity on the central motor nerve-cells, and some experiments on men go to show that the central nervous system is readily affected by fatigue products. On the other hand, there is the possibility that fatigue, if we look upon it as an inability to drive the muscular machinery up to its normal capacity, may be due to the deleterious influence of the products of muscular contraction on the end-plates. This view receives support from the fact that a fatigued muscle will contract by *direct* stimulation when it refuses to respond to a stimulus brought to it through its nerve.

Experiments on soldiers performing muscular work show how readily the intake of O_2 may be increased ; such causes as difficulties in the road, rising ground, increase in pace, change in the load carried, unpractised movements, even a sore foot, may increase the consumption by 18 per cent. Fatigue produces wasteful metabolism, and may increase the CO_2 excreted even as much as 21 per cent. The abnormal use of certain muscles, such as a man with sore feet would employ in order to save himself pain, produces extravagant combustion and fatigue. What applies to man in these matters applies equally to the horse ; ungreased axles, badly-fitting harness and saddlery, badly-made roads, sore backs and lameness, all represent undue muscular wear and tear. Fortunately we are indebted to the labours of Zuntz* for a more exact expression of the facts. He found a difference of 33 per cent. in the oxygen absorbed by two horses doing the same amount of work, and this difference was attributed to one of the horses being a high stepper.

The **nervous mechanism** connected with the use of the skeletal muscles cannot be considered here. The muscles have to produce two effects—viz., posture and movement. We shall see in the chapter devoted to the Nervous System that these are in essence reflex acts, for the mechanisms connected with movements and posture may be carried out even after removal of the brain. The question of muscular movement and attitude is of great practical importance, especially as affecting horses, while the experimental work, mainly carried out by Sherrington, by which the facts have been ascertained, have thrown remarkable light on the inner working of the nervous system.

Condition.—That remarkable state of the body described as ‘ condition,’ into which horses can be brought by care in feeding, general management, and carefully regulated work, must be regarded as the highest pitch of perfection to which muscles can attain. In its *highest* degree it is not a permanent state ; no horse can remain in it for any length of time, and many can never be got into condition for severe work. It is easy in the training

* *Op. cit.*

of horses to overstep the mark and produce 'staleness,' a result which, like the fatigued muscle on the myograph, is usually recovered from by a short judicious rest, to which the system immediately responds.

During training all superfluous fat and water are removed from the body, the muscle-substance is built up, and the respiratory capacity increased. It is very necessary to remember that condition, though judged of largely by the state of the muscles, has a very important claim on the respiratory and circulatory systems. To sustain severe and prolonged muscular exertion an adequate supply of oxygenated blood must be sent to the muscles; this necessitates a rapid flow of blood and adequate ventilation in the lungs, with strong regular pumping power in the heart; all these factors must work in harmony. As a matter of fact, the ability to endure the strain of a violent muscular effort is far more dependent on the training of the respiratory and cardiac mechanisms than on that of the muscles. Long walking exercise is given as a muscle developer, and judicious gallops to give an animal its 'wind,' yet as a matter of fact the 'wind' is largely a question of heart. As the circulatory pump works at high pressure, the bloodvessels must be fit to stand the strain and to return to the heart at both auricles the amount of blood leaving by both ventricles. A deficiency in this mechanism leads to 'loss of breath'; clogging in the lungs means deficient oxygenation in the tissues, and without an adequate supply of oxygen the muscles are powerless to contract. We are clearly shown, from what may be witnessed in the hunting-field, or wherever horses are exposed to long-continued strain, that the chief value in training is located in the functional improvement of the muscular tissue of the heart and in the circulatory system in the lungs; both of these have to be educated to withstand the extra strain imposed and to work economically. The voluntary muscles have also to be educated to work in the best and most economical manner; they must be used to advantage, smoothly and in combination; their response must increase in rapidity and power, while their relaxation must not be too prolonged and so cause loss of time. Unpractised movements are a serious source of waste; by practice the same amount of work can be performed with a reduced expenditure of energy, and this is true for both men and horses.

Sherrington* points out that in properly balanced muscular movements there is a period of rest between each successive contraction, which is recuperative in nature and opposed to fatigue. One feature in training, which will be more fully appreciated when the study of the nervous system has been made, is

* 'The Rôle of Reflex Inhibition,' *Science Progress*, No. 20, April, 1911.

the education of muscles in the importance of momentary rest following contraction, while the peculiar innervation of muscles, known as ‘ reciprocal,’ is also improved by education, and ensures that antagonistic muscles offer little or no resistance to their opponents.

There is additionally another factor of supreme importance in training. The respiratory movements, as we have learnt, are dependent upon the rhythmic activity of the respiratory centre (p. 133). Hence this centre must be taught to withstand the extra strain imposed upon it during violent exertion. What the centre has to ‘ learn ’ in respect of this is more or less a matter of conjecture. Bearing in mind the powerfully stimulating influence on the respiratory centre of the waste products of the metabolism involved in muscular contraction, it is conceivably possible that ‘ wind ’ is the result of an increased immunity of the centre to the action of these products. However this may be, one thing is certain—namely, that respiratory distress is more potent than most other factors in determining ‘ staying power,’ the one thing to which all long-distance athletes strive to attain. In this connection we may point out that it is said that the deleterious products of metabolism produced during fatigue may be neutralised and immunity established by giving small doses of extracts of a fatigued muscle ; the question has therefore arisen as to whether ‘ training ’ may not be a process of immunising against fatigue products.

Condition may also be defined as fitness for the class of work required, and one has only to think of the many uses to which horses are put to recognise that what constitutes fitness in one class, and for certain work, is unfitness for another. The circulatory and respiratory features of ‘ condition ’ have been referred to at p. 414 ; these constitute the basis on which the training of the machine is carried out ; but there is something more—there is the special education of the muscles for the particular class of work required. All muscles in the body are not equally conditioned, and this is forcibly brought home when for any reason uneducated muscles have to be employed. If a man uses his left limbs for services in which he always employs his right, his helplessness is at once manifest ; if he employs a group of muscles ordinarily idle, he is surprised at the effort required to extract any work from them and the feebleness of their response. The employment of muscles in this condition is a wasteful process, and until they are educated they cost more and do less work than the trained article. Each muscle has to learn how to perform effective work economically, and each group has to be instructed how to work harmoniously with other members of the group. The only way in which this education can be effected is by employing suitable resistance gradually and skilfully increased. Herein lies the art of the trainer, which requires a long education. The physiologist can control the process, for apart from gross errors in training, such as lead to horses refusing their food, there is the index afforded by the pulse and respiration as a measure of the progress made. In the following table is shown the mean of forty-five observations* on fit and a similar number of unfit horses performing identical work and carrying the same weight :

Average Pulse Rate before Work.	Average Respiration Rate before Work.	Pulse Rate at End of Work. (Taken for 15 Seconds.)			Respiration Rate at End of Work. (Taken for 15 Seconds.)		
		At Cessation.	Two Minutes after Stopping.	Five Minutes after Stopping.	At Cessation.	Two Minutes after Stopping.	Five Minutes after Stopping.
Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute
FIT HORSES.							
40	10	88	55	46	41	21	16
UNFIT HORSES.							
39	12	113	66	56	48	28	19

The table shows that the pulse and respirations of fit horses are less disturbed by work, and more rapidly subside to normal after work, than of those unfit. In the above series the heart and respiration rate of the 'fit' subsided in two minutes to a point only reached by the 'unfit' in five minutes.

Chemical Composition of Muscle.—A dead muscle does not possess the same chemical composition as one which is living, and living muscle cannot be analysed without killing it by the methods necessarily employed. Thus any tabular statement of the quantitative composition of muscle gives really the composition of dead muscle. We are, however, assisted to some knowledge of the nature of living muscle-substance by the following facts :

If contractile, and therefore living, frog's muscle is carefully frozen and then very slowly thawed, it does not lose its irritability : it is still alive. When frozen it may be minced with a cold knife and ground up in a cold mortar with four times its weight of snow containing 1 per cent. of sodium chloride. By this process a viscid liquid is obtained which may be filtered, though with difficulty, at 0° C. The fluid filtrate is opalescent, neutral, or faintly alkaline in reaction, and is known as 'muscle-plasma.' When its temperature is allowed to rise it coagulates in the same way as does blood-plasma, yielding a *clot* which, unlike fibrin, is granular and flocculent, and forming a liquid *serum*. During the clotting the liquid becomes acid, as the result of a formation of *sarcolactic acid*, and the clot consists of *myosin*. Assuming, as we may reasonably do, that the muscle-plasma represents more or less closely the muscle-substance in the living fibre, we may take these phenomena of the clotting of the muscle-plasma as indicating the most characteristic chemical differences between living and dead muscle (though there are others), and thus we gain considerable insight into the composition of living muscle as based upon an analysis of the dead tissue.

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* Made for the writer by Captain Wadley, A.V.C.

With this preliminary caution we may now state the composition of muscle to be approximately as follows :

Water	75	per cent.
Proteins	20	,,
Fat	3	,,
Carbohydrates	0·4 to 1	per cent.
Nitrogenous waste products	0·2	,,
Salts	1 to 1·5	,,

Our knowledge of the nature of the proteins of muscle is a matter of no slight uncertainty, which is not made less by the existing confusion in the terminology employed by various investigators. Into this we cannot here enter. It must suffice to say that the chief and characteristic protein of dead muscle is the *myosin* formed in the clotting of muscle-plasma ; it belongs typically to that class of proteins known as *globulins*. Bearing in mind the phenomena of the clotting of muscle-plasma, and using the nomenclature employed for blood-plasma, we may say that living muscle contains *myosinogen*, which on the death of the muscle is converted into myosin, just as in blood-plasma fibrinogen gives rise to fibrin. It has not as yet been shown that calcium salts play a part in the coagulative formation of myosin, as they necessarily do in the case of fibrin and of the casein-clot in milk. The proteins of living muscle are not entirely myosinogen, nor are those of dead muscle entirely myosin. Other members of the globulin class are present in both, as also an ordinary albumin closely resembling serum albumin.

The carbohydrate material is composed chiefly of glycogen, which diminishes in amount by conversion into sugar on the death or after the contracting activity of muscles ; these substances have already been fully dealt with in a previous chapter. The nitrogenous waste products or 'extractives' are kreatin, hypoxanthine (obtainable in the free form in muscle extracts), xanthine, carnine, taurine (in horse-flesh), uric acid in minute traces (though more abundant in reptilian muscle), and traces of urea, though this is a question still not decisively settled. Of these kreatin is by far the most important ; it is a substance which has already been studied in connection with the production of urea (p. 325). The ash in muscle consists principally of the salts of potassium and magnesium. The gases are carbon dioxide, together with a small amount of nitrogen, but no free oxygen. In plain muscle glycogen is only found in traces, if at all ; lactic acid and kreatin are found in smaller quantities than in striped muscle. Hypoxanthine is conspicuously present. As just stated, potassium and magnesium furnish the chief salts of striped muscle, while salts of sodium and calcium represent those of plain muscle.

Rigor Mortis.—After death a muscle passes into the condition of rigor or stiffening, by which it changes both in its physical and chemical aspect. The muscle becomes firm and solid, loses its elasticity, and no longer responds to electrical stimuli ; further, it loses its alkaline reaction, and in course of time becomes acid owing to the formation of sarcolactic acid. Through the death of the muscle its proteins pass from a fluid or viscous condition into a solid, and this process is generally believed to be identical with the clotting of muscle-plasma previously described. Rigor mortis and the production of sarcolactic acid are closely connected, so that if the formation of the acid be prevented by suitable means, rigor does not occur. The view now adopted as to the cause of death-stiffening is that it is due to a coagulation of the proteins by the products of metabolism in the muscle, and this explanation accounts for the rapid setting in of rigor in animals hunted to death. Rigor mortis is delayed in a rabbit in which the labyrinth of the internal ear has been destroyed. This is probably connected with the obscure problem of muscle tonus, with which the labyrinth is connected. The muscles in which delayed rigor mortis occurs are those corresponding to the same side of the body as the injured labyrinth. During rigor mortis carbon dioxide is produced and heat evolved ; some after-death temperatures are remarkably high. After a certain length of time rigor mortis passes off and decomposition commences.

There is a condition of muscle known as **heat rigor,** which is produced by rapidly raising the temperature of a mammalian muscle to 47° C. (117° F.). It is very closely allied to death rigor, and is due to the same cause—viz., coagulation of the proteins. It differs from death rigor inasmuch as it does not pass away.

It is doubtful whether rigor mortis occurs in involuntary muscle ; the appearance presented in this variety of muscle may be due to cold, for it has been shown that two or three days after death smooth muscle may be warmed up so as to be capable of contraction.

Phenomena of Contraction in Smooth Muscle.—Though there is a marked difference in appearance between red and smooth muscle, the actual phenomena of contraction do not differ excepting in the matter of rate. The latent period, contraction, and relaxation, are present, as in red muscle, but occur more slowly ; they are, in fact, sluggish and deliberate. Owing to the existence of numerous nerve fibres and ganglia, smooth muscle may be completely isolated from all nervous connections, and still continue to exhibit the phenomena of muscular contraction.

In response to a continuous or induced current, smooth muscle behaves much as does red, excepting, of course, that the response is slower—as much as from 100 to 500 times slower. Summation also is present, though not identical with that observed in red muscle, for no contraction follows the first three or four stimuli ; it is the stimuli which here accumulate before contraction follows, and after this has occurred the muscle subsequently responds to further stimuli by an increased height of contraction as does a red muscle.

Mechanical stimulation of smooth muscle excites a sluggish but marked response ; pinching the intestines produces peristalsis, and even drawing the finger lightly over the stomach wall may produce ‘ weals ’ of contraction. The muscle is markedly responsive to tension, resembling in this a skeletal muscle which, as we have seen, up to a certain ‘ load ’ does more work the greater the weight it has to lift. In the case of the smooth muscle of the digestive canal the chief source of stimulation in the herbivora lies in the cellulose and indigestible fibres in the food, the bulkiness of their diet providing the mechanical stimulation and distension necessary to produce the tension to which this muscle is so responsive. The same remark may also apply to the physiological action of the stomach and intestinal gases ; nor must the bladder be omitted from this consideration, from the point of view that distension by fluid provides a tension of the walls which acts as a stimulus to contraction. There are two distinctive physiological features associated with smooth muscle, one is its capacity for remaining contracted for a long period, and the other is its rhythmical activity.

CHAPTER XIV

THE NERVOUS SYSTEM*

SECTION I.

Classification of Nerves.—The first step towards a classification of nerves was taken when the discovery was made that some nerves are exclusively sensory and others exclusively motor in function ; prior to this it was believed that a nerve could carry either impulse indifferently. It was next found that a nerve in the body could only carry impulses in one direction ; for instance, a sensory nerve could only convey impulses from the periphery of the body towards a centre, a motor nerve could only convey impulses from a centre to the periphery. This is the real basis of classification, notwithstanding the fact that the impulses travelling to a centre, though spoken of as sensory, may be widely different in nature, and those from a centre to the periphery, though motor, may only be so in an opposite sense. The terms ' sensory ' and ' motor ' prove very misleading in speaking of the function of a nerve, and for long it has been recognised that the two great divisions of nerve fibres are **afferent,** or centripetal, and **efferent,** or centrifugal. An afferent nerve is one conveying impulses from the periphery to the centre, no matter what the nature of these impulses may be. An efferent nerve is one conveying impulses from a centre to the periphery, notwithstanding that these impulses may be of widely different characters. The determining factor of whether a nerve is afferent or efferent does not lie in its structure ; there is no microscopical difference between the two. The real explanation lies in the nature of the nerve-ending in the tissues, and this is proved by the fact that one kind of efferent nerve may be made experimentally to take the place of another.

Afferent nerves, as we have seen, are those engaged in conveying impulses towards a centre ; the centres are the brain, spinal cord, and masses of nerve tissue connected therewith, known as 'ganglia.' Whether the afferent nerves be those of special sense —*i.e.*, visual, olfactory, gustatory, and auditory—or those of touch, pressure, heat, cold, and pain, the widely different results obtained on stimulation depend upon the end-organ of the nerve, and not on any difference in the character of the impulses. There are afferent impulses constantly occurring which are not within the knowledge of the animal; they may be of an excitatory nature, or of a controlling or inhibitory character. We have studied this group characteristically in our consideration of the vascular and respiratory system, pressor or depressor effects occurring in the circulation in consequence of excitatory or inhibitory impulses conveyed by afferent nerves, though not necessarily by the same afferent nerve. The same occurs also in the respiratory system. Nor are we in this question limited to the two systems mentioned; we have met with it in muscle-tone, visceral movements, glandular secretion, and in other ways. **Efferent nerves** are those in which the impulses are passing from the centre to the periphery, and the largest system of efferent nerves in the body is that passing to the muscles. The term is used in its widest sense, for not only are the skeletal muscles richly supplied, but also, as we have already seen, the unstriped muscle of the viscera, bloodvessels, and body hairs, and the striped muscle of the heart. Nor are efferent impulses solely motor; they may be secretory. We have studied this in connection with saliva and gastric juice. Finally the impulses may be inhibitory, and control or prevent muscular movement, and control or prevent secretion.

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* I am indebted to Professor Sherrington, F.R.S., for kindly reading this chapter and supplying that portion dealing with the ' scratch,' and ' step ' reflex.

It must not be supposed that all the tissues of the body are completely endowed with the nerve fibres described. Fibres for the bloodvessels, excitatory and inhibitory, are not found in all bloodvessels, and though excitatory efferent (motor) fibres exist largely in skeletal muscle, there are no inhibitory fibres to this tissue, a remarkable fact, which will be fully considered later, in view of its extraordinary physiological importance.

From the above it will be seen that a classification of nerves is not a simple matter, and physiologists are not agreed as to the best system to adopt. The afferent scheme given on p. 422 has been suggested by Professor Sherrington.

Personally we would add to the classification *trophic* nerves, or those engaged in nutrition. Some physiologists hold that special nerves governing nutrition do not exist, and that the process runs concurrently with the nerves governing wear and repair. The existence of nerves specially provided for nutritional purposes is not perhaps generally accepted; the evidence that exists in their favour will be mentioned in due course.

AFFERENT NERVES.*

	Peripheral Distribution.		Sensation.			Stimulus.		Reflex Effect.
	General.	*Local.*						
I. From *surface* of organism	External (or cutaneous) surface, including mouth (*exteroceptive*)	Skin	Pain		Stimuli are all environmental	Any stimulus, chemical, thermal, mechanical, or electrical, so long as injurious (*nociceptive*)	Sensory and reflex effects both ample—*i.e.*, cerebral and post-cerebral reactions both intense	Postures and movements by skeletal muscles; circulatory and respiratory muscles.
			Warmth Cold			Temperature	.. ..	Circulatory, respiratory, and pilomotor muscles; sweat glands.
			Touch			Mechanical	Sensory effect more marked than reflex—*i.e.*, cerebral reactions > post-cerebral	Skeletal muscles.
		Cochlea	Distance sensations	Auditory		Mechanical (sound)		Muscles of ear, neck, and eyes.
		Retina		Visual		Radiation (light)		Muscles of eyes and neck.
		Nose		Olfactory		Chemical vapours and solutes	.. ..	Respiratory muscles; salivary and gastric glands.
		Tongue and palate	Taste			Chemical solutes	Sensory and reflex effects both marked: cerebral = post-cerebral	Muscles of mastication and deglutition; salivary and gastric glands.
	Internal (or digestive, urinary, and respiratory) surface (*interoceptive*)	Alimentary canal (fauces to anus)	None (? repletion and emptiness): abnormally pain		Stimuli are contents—*e.g.*, food, etc.	Mechanical and chemical	Sensory effect much less than reflex: cerebral reaction < post-cerebral	Visceral movements and secretions; circulatory changes, local and general.
		Respiratory tract	None: abnormally pain			Mechanical and chemical	Ditto	Respiratory muscles.
II. From *depth* of organism (*proprioceptive*)		Labyrinth (ear)	Sensations of positions and motions of head (abnormally vertigo)		Stimulation always, some part of the body itself acting as stimulus to the body's own receptors—*i.e.*, *proprioceptors*	Mechanical	.. ..	Postures (muscle-tone) and movements of eyes, head, and neck, and, to less extent, of limbs and trunk.
		Skeletal muscles (including tendons) joints and fasciæ.	Sensation of positions and motions of body and limbs—*i.e.*, muscular sense: abnormally cramps			Mechanical, chiefly stress or strain	Sensory effect less marked than reflex—*i.e.*, cerebral reaction < post-cerebral	Postures (muscle-tone) and movements of neck, trunk, and limbs: tendon reflexes, knee-jerk, etc.
		Visceral and circulatory muscles	None: abnormally cramps			Mechanical, chiefly distension	.. ..	Alterations of tone and rhythmic contraction of the visceral or circulatory muscles involved.

- Efferent
  - Pressor
    - Motor
      - Motor to skeletal muscle.
      - Vasomotor.
      - Cardio-motor (not a true motor).
      - Viscero-motor, and includes respiratory (trachea and bronchi) and coat of spleen.
      - Pilo-motor and unstriped muscle of skin generally.
      - Iris and ciliary muscle.
    - Secretory
      - Salivary.
      - Gastric.
      - Sudorific.
  - Depressor
    - Inhibito-motor
      - Only known for heart, some bloodvessels, some parts of digestive canal, iris, and retractor penis.

Conduction in Nerves.—In considering the direction of the impulses conveyed by nerves as a basis of classification, there are two fundamental principles on which something more should be said. It has been shown that the effect produced by a nerve does not depend upon its structure, but upon the nature of its termination in the tissue. Many years ago, before the truth of this doctrine had been conclusively established, the writer had endeavoured to cure a local paralysis by dividing the paralysed nerve and suturing the peripheral end to the central end of a sound motor nerve. He found that when two sound nerves were so dealt with motor impulses from an entirely new source provided the tissue with motor function, and, moreover, furnished it at the right moment—viz., at the moment the muscle was required to contract, and not during the period when it should relax. Subsequently Langley showed by a similar experiment that the function of the chorda tympani and sympathetic on the bloodvessels of the submaxillary gland could be reversed. If the peripheral end of the sympathetic were united to the central end of the chorda, the effect was constriction and not dilatation of the vessels. Similarly, if the peripheral end of the chorda were united to the central end of the sympathetic the vessels dilated on stimulation of the sympathetic instead of contracting. The essential structure was proved to be the nerve termination in the tissue, and not the nerve which carried the impulse.

It is on these lines that the writer has looked for the cure of laryngeal paralysis in horses. But though he has succeeded, as stated above, in getting a sound left recurrent sutured to a sound spinal accessory to function properly, he has not succeeded in obtaining these results with a paralysed left recurrent, not even when the operation has been performed early, presumably before the end plates had undergone complete degeneration.

The other fundamental principle in nerve conduction relates to the law that the living nerve only transmits impulses in one direction—viz., either to the centre or to the periphery. When a nerve is removed from the body there is no difficulty in transmitting an electrical impulse in either direction, but within the body the law is as stated. We shall see presently that the dorsal roots of the spinal cord are sensory or afferent, but Bayliss has shown that if these roots from the fifth lumbar to the first sacral be divided, and the *peripheral* end stimulated, vascular dilatation of the vessels of the hind-limbs occurs. The assumption is, therefore, that efferent fibres are passing out of the cord through the dorsal roots, and conveying motor impulses to the bloodvessels in a direction opposite to that in which the ordinary sensory impulses pass. Bayliss has termed these impulses *antidromic*, as indicating they are occurring in the opposite direction to the natural stream.

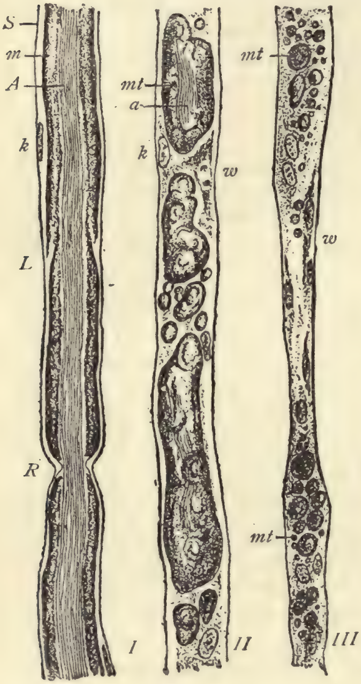

FIG. 124.—NORMAL AND DEGENERATED NERVE FIBRES (BARKER, AFTER THOMA).

I. Normal fibre: *S*, neurilemma; *m*, medullary sheath; *A*, axis cylinder; *L*, Lantermann's line or cleft; *R*, node of Ranvier. II. degenerating fibres: *mt*, drops of myelin; *a*, remains of axis cylinder. III. further stage of degeneration: *mt*, drops of myelin; *w*, proliferating cells of neurilemma.

Structure of Nerves.—Nerves were originally grouped under two heads, according to their colour, as *white* and *grey*. The microscope revealed the fact that a difference in structure existed between them, the white fibres possessing a thick coating of fatty substance which gave them their colour, while the grey fibres were without this covering. The white substance is described as the medullary sheath; nerves so covered are termed *medullated*, while the 'grey fibres'—a term now rarely used—are spoken of as the *non-medullated*. If a **medullated nerve** be examined microscopically (Fig. 124, I), it is found to consist of a central core, or *axis cylinder*, consisting of fibrils, surrounded by a white substance known as the *medullary sheath*, and outside this is another sheath, or *neurilemma*. The medullary sheath does not extend continuously along the nerve; it is broken at intervals, termed *nodes.* The portion of nerve included between two nodes has a nucleus somewhere in it lying beneath the neurilemma. A bundle of such fibres enclosed in a sheath—and they may number thousands to the bundle—constitutes a nerve. A **non-medullated nerve** resembles the above in every respect, excepting the medullary sheath. Of this it has none. It consists of an axis cylinder covered by a neurilemma. The fibre is freely nucleated, and a bundle of such fibres in a sheath constitutes a non-medullated nerve. This class of nerve belongs solely to one branch of the nervous system—viz., the sympathetic—whereas the medullated fibres are confined to the larger system of cerebro-spinal nerves.

The essential feature in the nerve is the axis cylinder ; it is the true impulse-conducting substance. The function of the medullary sheath is not definitely known, and it has been assumed to play the part of a non-conductor and insulate one fibre from another ; but evidently this does not exhaust its uses, for, as just mentioned, the fibres of the sympathetic system are without a medullary sheath. Even medullated nerves lose their sheath before terminating in the tissues. Medullated nerves are more sensitive to stimuli than non-medullated, and the longer the nerve the greater the thickness of the sheath, but at present these facts cannot be connected with its function.

The axis cylinder, as previously stated, is *the* important part of the nerve ; it is the conducting substance, and its nature and origin are of the utmost significance. We shall see presently that the entire nervous system consists of nerve-cells and fibres. The nerve-cell is the essential feature, and no matter whether the brain, spinal cord, or ganglia be examined, nerve-cells characteristic of the tissue are present ; the nerve-cells of the cerebellum are absolutely distinct from those of the cerebrum ; the cells in the ganglia are different from either, or from those found in the spinal cord. It does not matter how greatly the nerve-cells differ in type, they all conform to one law, and that is they each furnish from one pole of the cell a process which becomes a nerve-fibre. No cell furnishes more than one such process, and that process constitutes the axis cylinder of the nerve. When the neurone doctrine is dealt with, more will be said on this subject, but one piece of information must be anticipated, and that is a nerve-fibre is really an elongated process of a nerve-cell, and may run for a considerable distance without a break ; even when it is broken the thread is again taken up, so that the axis cylinder runs from its origin to its termination. There is no union of nerve-fibres ; of the thousands in a large bundle each and every one is complete in itself, and it is this which enables the same nerve-trunk to convey impulses of many and opposite kinds, of which no better example could be given than that of the vagus, with its fibres to the larynx, lungs, heart, stomach, and intestines, each functioning in its own way and independently of its neighbour, with which it may have no more in common than if it never existed.

Nerves are remarkable for their want of elasticity, but they are capable of very considerable stretching without breaking. In man the nerves of the limbs require a weight of from 18·2 kilogrammes (40 pounds) to 54·6 kilogrammes (120 pounds) to break them. Nerves are also very indifferently supplied with blood-vessels.

Nerve Terminations.—There are some structures, such as glands, where the nature of the nerve termination is not satisfactorily made out; there are other places, such as muscle, where definite and distinct motor nerve-endings have been found; and on many sensory and sympathetic nerves special terminations, known as 'Pacinian corpuscles' and 'Krause's end-bulbs,' exist. Nerve terminations are found in the muzzle of animals, in tendons, in muscles, in the generative organs, conjunctiva, mouth, tongue, epiglottis, etc.; some are known as 'Krause's end-bulbs,' those in tendon are described as the 'organ of Golgi,' in muscle they are known as 'end-plates,' whilst in the skin of the muzzle the nerves terminate in small swellings or enlargements known as 'tactile cells,' which are placed between the epithelial cells of the epidermis; cells of this kind also exist in the foot of the horse. The nerves of special sense have each a distinct termination peculiar to themselves, such as the hair-cells of the internal ear, the rods and cones of the retina, taste-bulbs of the tongue, etc.

Chemistry of Nerve-Fibres.—The chemistry of these tissues is very imperfectly known. Advances in physiological chemistry have shown that substances like *protagon*, which at one time was believed to represent the essential composition of the medullary substance or myelin, are really a mixture of substances. The myelin furnishes three substances which possess definite chemical characteristics—viz., cholesterin, lecithin, and cerebrosides. *Cholesterin* is a substance containing neither nitrogen nor phosphorus, and in chemical nature is allied to a group of bodies found in plants known as *terpenes*. Its silvery crystalline formation is characteristically shown in the tumours on the choroid plexus of the horse. In the body it occurs with lecithin, though the nature of the physiological connection, if any, is unknown. *Lecithin* is a phosphorus-containing nitrogenous fat, especially characteristic of the nervous system, but found elsewhere in the body. When lecithin is decomposed it yields, among other products, a fatty acid; it is this which is blackened in osmic acid staining of normal and degenerated fibres. *Cholin*, another product of the decomposition of lecithin, is very poisonous. *Cerebrosides* are a group of glucoside bodies containing nitrogen, of which very little is known, excepting that they yield galactose on decomposition.

Irritability and Conductivity.

Two features of nerve-fibres are irritability and conductivity. By irritability is understood the reaction to a stimulus, by conductivity the propagation of an excitation. The nature of the change occurring in a centre or receptive surface which induces an impulse is as yet unknown, but whatever the change may be it is experimentally possible to imitate it artificially by means of chemical, mechanical, or electrical stimuli, and when nerves are so stimulated they function as if the normal stimulus had been applied. Electrical stimuli are most commonly employed, and if a motor nerve be so stimulated the muscle contracts ; if a sensory nerve, pain or a sensory impression is observed. If a secretory nerve be stimulated, secretion results. At one time the normal stimulus to a nerve-cell was believed to be electrical in nature ; it is now known that this is not so, and that though electrical stimuli are capable of causing a nerve to function, it is a coarse method compared with the natural stimulus. A sudden change in temperature acts as a stimulus to a sensory, but not to a motor nerve. A motor nerve is quite unaffected by sudden cooling or heating, whereas a sensory nerve so treated produces pain, and it has been suggested that this difference in reaction indicates some marked difference in structure. When nerves are ligatured or divided impulses are no longer transmitted. Experimental inquiry shows that even after long-continued excitation nerves are still irritable, which has given rise to the belief that nerves never suffer from fatigue (see p. 432).

When dealing with the question of muscular contraction (p. 395), it was stated that the stimulation of a nerve-muscle preparation by means of a constant current caused a ' twitch ' of the muscle at ' make,' and another at ' break,' and that during the period the current was passing through the nerve, though the muscle gave no evidence of this, yet important changes were occurring. These changes are concerned with the irritability and conductivity of the nerve, and must here be examined.

Electric Phenomena in Nerves.—When studying a muscular contraction, we saw that a perfectly uninjured muscle was *iso-electric* —viz., it gives no evidence to the galvanometer of the existence of a current. If, however, the muscle be injured, the seat of injury became electrically negative to the uninjured part, and the current was called the **current of injury.** The figure there employed to explain injury currents in muscle is again used here to explain the same currents in nerves. If the nerve be injured, the current of injury flows from the equator to the cut end outside the nerve, and from the cut end to the equator inside the nerve. If a nerve, while exhibiting the presence of a current of injury, be stimulated, the uninjured portion becomes electrically negative to the injured part. There are now two currents in the nerve—viz., the current of injury and the new one just created; each is flowing in the opposite direction, the result being that the current of injury becomes diminished. This diminution or reduction in the current of injury is termed **negative variation.**

In the two observations described the nerve is assumed to be in an injured condition. If now a constant current be passed through an uninjured nerve, a wave of electrical negativity travels along it, and this current is termed the **current of action.** It will be obvious that it was the presence of the current of action which diminished the current of injury in the previous experiment. Let a nerve be taken and arranged as shown in Fig. 126, A—viz., a constant (polarising) current passed through its middle piece, while a galvanometer is connected with both regions of the nerve outside the anode and kathode poles of the battery. Under these circumstances, a polarising current passes through the nerve in the direction of its circuit—viz., from anode to kathode and back to the battery; but, in addition to this, there is a current in the extra-polar regions, as indicated by the attached galvanometers. These extra-polar currents are termed **electrotonic.** The piece of nerve beyond the kathode is increased in excitability and conductivity, and this is termed *kathelectrotonus*. The portion of nerve beyond the anode is decreased in excitability and conductivity, and is in a condition known as *anelectrotonus*. It will be observed that, though the battery current

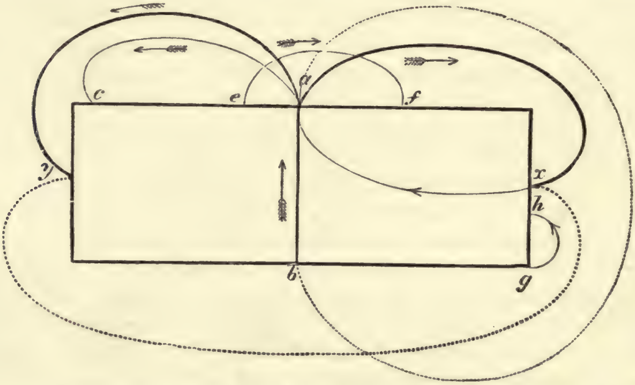

FIG. 125.—DIAGRAM ILLUSTRATING THE ELECTRIC CURRENTS OF INJURY IN NERVE AND MUSCLE (FOSTER).

The diagram serves either for nerve or muscle, excepting that the current *gh* is not present in nerve. The strong currents are shown by the dark lines; the arrows show the direction through the galvanometer. *ab*, The equator; *ax*, current from equator to cut end; *xa*, current within the nerve, cut end to equator.

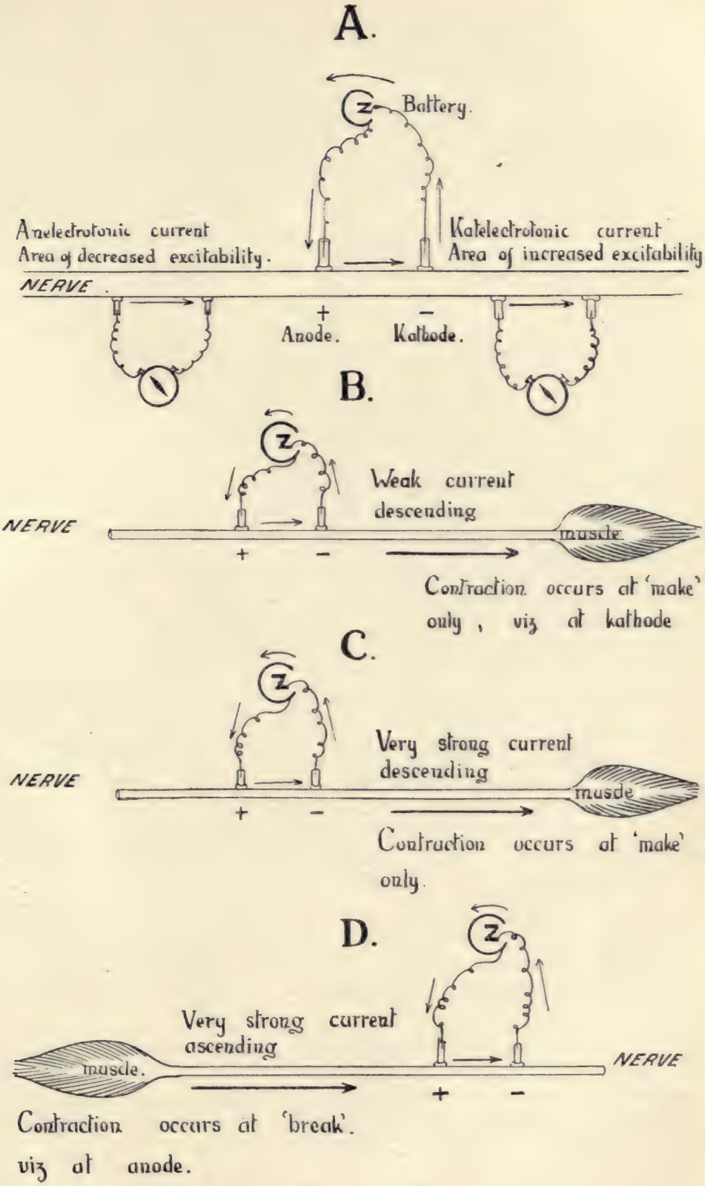
A.
Battery.
Anelectrotonic current
Area of decreased excitability.
Katelectrotonic current
Area of increased excitability
NERVE.
+
Anode.
–
Kathode.
B.
NERVE
Weak current
descending
muscle
+
–
Contraction occurs at 'make' only, viz at kathode
C.
NERVE
Very strong current
descending
muscle
+
–
Contraction occurs at 'make' only.
D.
Very strong current
ascending
muscle.
NERVE
+
–
Contraction occurs at 'break'.
viz at anode.

Fig. 126.—Diagram of Electrotonus.

is only sent through the middle piece of the nerve, it gives rise to a current which passes through the whole length of the nerve in the same direction as the exciting current, as shown by the galvanometers. Turning again to Fig. 126, A, it is evident that between the region of increased and that of reduced irritability there must be a region of neither increased nor diminished irritability. This is known as the *neutral point*. When the polarising current is weak, this point is nearer the anode ; when it is strong, it is nearer the kathode, so that with very strong currents the whole intrapolar region may be in a condition of anelectrotonus. A clear understanding of this fact will render the subsequent observations intelligible. It will be remembered that the muscle of a nerve-muscle preparation gave, on stimulation, a twitch at 'make,' and another at 'break,' the make contraction always starting from the kathode, and the break contraction from the anode. These contractions are due to the development of electrotonic currents, and, provided the stimulating current always remains of the same strength, the twitch at 'make' and another at 'break' will always be obtained. But it is known that an increase or decrease in the strength of the polarising current gives other results in the muscular response ; for instance, if the current be weak (Fig. 126, B), contraction of the muscle only occurs at 'make,' the kathode end of the nerve being the region of increased excitability and conductivity, the anode end being in both these respects decreased, and with a weak current lowered below the point of possible electrical response. If the current be made stronger, contraction occurs both at 'make' and 'break.' If a very strong current be passed through the nerve, contraction occurs at 'make' only, owing to the neutral point moving nearer the kathode, and so diminishing the irritability of the anode pole (see Fig. 126, C). If the muscle be attached to the opposite end of the nerve—viz., nearest the anode pole—and a very strong current sent through, the battery current will be passing up the nerve, as it is termed—*i.e.*, from the muscle to the spinal cord (Fig. 126, D)—under these conditions there is no difficulty in a 'break' contraction occurring, as the muscle is nearest to the battery current ; but the reduced excitability and conductivity of the nerve prevents the current from reaching the kathode, so that no contraction occurs at 'make.' Pflüger, who investigated these phenomena, formulated a **Law of Contraction,** which, after the above explanation, may now be stated :

Strength of Current.	Ascending Current.		Descending Current.	
	Making.	Breaking.	Making.	Breaking.
Weak -	Contraction	No contraction	Contraction	No contraction
Moderate	Contraction	Contraction	Contraction	Contraction
Strong -	Contraction	No contraction	No contraction	Contraction

When a particularly irritable nerve-muscle preparation is stimulated with a constant current, it may pass into tetanus at either 'make' or 'break.' This is known as *Ritter's tetanus*. The nature of electrotonic currents is not fully agreed upon; they are markedly shown in fresh medullated nerves, but not in those which are dead; they are only feebly shown in non-medullated nerves. Though physical in origin, they can only be obtained in nerves which still possess the characteristics of living. They may be demonstrated in an artificial nerve in which the axis cylinder is represented by platinum wires, and the medulla by a glass tube containing a solution of zinc sulphate. It is believed that electrotonic currents are due to polarisation occurring between the medullary sheath and axis cylinder, but nothing is yet settled.

The facts which have been ascertained experimentally as to effects which follow the application of constant and induced currents have been employed in the diagnosis of nerve degeneration. A healthy motor or sensory nerve, or healthy muscle, reacts to both stimuli. A degenerated nerve conveys no sensory impulses, nor is stimulation of a motor nerve so affected followed by muscular contraction. Muscles in the horse, other than as the effect of azoturia, do not appear to suffer from atrophy, excepting as the result of injury or degeneration of the nerves. A muscle will grow smaller if thrown out of use, but the result is very different from the atrophy occurring in consequence of nerve degeneration, which is remarkable for its completeness and the relative rapidity with which it occurs. Muscle fibres will respond to direct stimulation of a constant current, even when the nerve is degenerated; but the contraction is slower, and is not brought about through the nerves, but through the muscle fibres. A healthy muscle responds as readily to a constant as to an induced current. With complete degeneration of a motor nerve, no response on stimulation is evoked from the muscle; nor can the latter be stimulated by induction shocks, but it may be stimulated by the constant current. This is employed in human practice as a test of degeneration. A normal contraction, we have seen, occurs at the negative pole on closing. To obtain a contraction at the positive pole on closing, a stronger current must be employed; but in paralysis, which is not of central origin, the muscles do not respond to an induced current, but react to a continuous current, and the same strength of current, both of opening and closing, will readily produce a response. This is the *Reaction of Degeneration.*

Negative Variation.—We have seen (p. 428) that when a nerve is indicating through the galvanometer the existence of a current of injury, its stimulation leads to a current in the opposite direction, or negative variation. In living nerves negative variation has been observed in consequence of stimulation of the brain, and the association of negative variation with normal nerve impulses is accepted. Negative variation marks in a nerve what a contraction represents in a muscle—viz., the passage of an impulse. The capillary electrometer shows that the onward rush of negativity travels at the same rate as a nerve impulse. By means of the string galvanometer of Einthoven (an instrument far surpassing the capillary electrometer in delicacy), a negative variation may be seen to occur in the vagus at each inspiration. Movements due to an electrical change can be detected passing both up and down the nerve in consequence of nervous impulses.

Diphasic Variation.—When a muscle contracts, a wave runs along it, and an electrical change occurs. The contracting part of the muscle becomes more positive, and then, as the muscle returns to the state of rest, this positivity disappears (see p. 407). This two-phase electrical condition is termed *diphasic variation ;* its presence in muscle is concurrent with a contraction, while in nerve it is identical in point of time and rate with the transmission of a nervous impulse. We have seen that the current of injury may be detected by the rheoscopic frog ; the current of action may be detected in the same way. If the nerve of a nerve-muscle preparation be laid on the heart of a frog which is still active, the current of action liberated from the heart by its contraction causes the muscle of the limb to contract at each heart-beat.

The string galvanometer shows that when a muscle contracts two electrical waves pass over it, due to changes in potential. Electrometer records of the contraction of the heart muscle may be obtained by placing leads either on the exposed heart, or leading off through the limbs. Waller was the first to show how an electrocardiogram could be obtained in an intact animal at each beat of the heart. If a dog be placed with one fore-paw in a basin containing a solution of salt, and a diagonal hind-paw in another, and the two basins connected with the galvanometer, at every beat of the heart the electrical changes resulting from its contraction are conducted through the body to the electrometer, and the minute movements of the mercury rendered visible by a microscope. Contraction begins at the base of the heart ; the base is therefore negative to the apex. When the ventricles contract, the cardiogram shows that the apex is then negative to the base ; the interpretation of the curve is not, however, so simple as might appear.

Nature of Nerve Impulse.—The velocity of a motor impulse in man has been ascertained to be about 100 metres (333 feet) per second ; the velocity in sensory fibres is unknown. In the frog the velocity of the action-current in motor nerves agrees exactly with the rate at which a motor impulse travels in the animal, and in discussing the nature of nerve-impulses it is natural that the action current, or negative variation, should be considered to be intimately connected with the transmission of ordinary normal impulses. It is known that in the case of the passage of impulses along the optic nerve, or of light falling on the retina, these are accompanied by electrical changes. Action-currents can be obtained in motor nerves on stimulation of the cerebral centres governing limb movements ; currents of action can also be demonstrated in the living muscles of the limbs ; diphasic variation of the working heart can be recorded ; and it seems generally accepted that the passage of an impulse along a nerve is associated with an electrical change, though it is necessary to be careful and to avoid considering this change and a nerve impulse as identical. Hitherto it has been usual to regard a nerve-fibre as not suffering from **fatigue** ; the end organ, it was known, could be exhausted, but not so the nerve. This view was arrived at in consequence of the non-existence of chemical products arising from the passage of impulses, the presence of which would suggest that conduction was a question of chemical activity. The fact that the passage of impulses excites no apparent consumption of material, no heat, and, so far as can be determined, no fatigue, places nerve in a special class, for there is no other tissue in the body which does not show signs of fatigue when constantly stimulated. Yet there is some evidence that a nerve does not entirely escape from the effects of work. There is a 'refractory period' found to exist in nerves which have been stimulated for some time, and a nerve kept in an atmosphere of nitrogen loses its irritability, and rapidly so, if constantly stimulated. It is therefore suggested that ordinary fatigue products may be rapidly oxidised in nerve, and so no accumulation and consequent fatigue is possible. The view which at the present time receives the most favour is that nerves are capable of being fatigued, but so rapidly is the process of repair carried out that fatigue properties are not exhibited.

It is believed that the nature of the impulses in all nerves is the same, but that the differences in the results obtained depend upon the termination of the nerves in the tissues (see p. 423).

The Neurone Doctrine.—It is only within the last twenty years that it has been possible to visualise the elements concerned in the working of the nervous system, not only with regard to their structure, but also their function. That the nervous system consisted of fibres and nerve-cells had long been known, that the cells were capable of nourishing the fibre was shown years ago by the experiments of Waller on the dorsal roots of the cord, but there was something lacking. The origin of the nerve-fibres was unknown, while the distribution of the cells in the grey substance did not appear to be arranged on any system connected with a physiological basis. The doctrine of the neurone supplies what was wanting. A neurone is a nerve-cell, with its various processes and nerve-fibres. The cell-body,* the fibre, and the processes are a physiological unit, a nervous system in miniature; myriads of such microscopic systems constitute the nervous system.

A **nerve-cell** consists of a mass of protoplasm intersected by fine fibrils known as neuro-fibrils. Towards the centre of the cell is a refractile nucleus, and lying between the neuro-fibrils are certain peculiar bodies, which, though granular in nature, stain with methylene blue, an exception to the general staining reactions of cell granules (Fig. 127). These bodies are known as *Nissl's granules*, or *chromophile substance*; they exist in the form of angular-shaped masses or rods, and extend into all the processes of the cell, excepting that from which the nerve-fibre arises. These granules are intimately concerned in the nutrition of the cell and its fibre, but whether as fluid or granules is unknown. In a working cell the granules diminish, and under great muscular exertion they may be reduced to fine particles, resembling dust in appearance. This is due to the chromophile substance breaking up; the chromatolysis so produced also occurs when the cell is separated from its fibre. It is evident from this that nerve-cells, unlike nerve-fibres, are capable of fatigue. Nerve-cells are not all of the same shape, size, or general arrangement; some have only two processes growing from the cell, and hence are called 'bipolar cells'; other cells have numerous processes, and are called 'multipolar.' All the processes of a nerve are not nerve-fibres; of all the processes in the multipolar cell shown in Fig. 129 only one is the beginning of a nerve-fibre. It is called the **axon**; it is the process of the cell which transmits the impulse. The other processes are called **dendrites**; they are the receiving portion of the cell. The actual conducting materials in the cell are the

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* The '*nerve-cell body*' and the '*nerve-cell*' are not the same; the latter includes the dendrites and axons—it is, in fact, the neurone. The former is the cell which gives birth to the neurone, and it is best distinguished as the *perikaryon*.

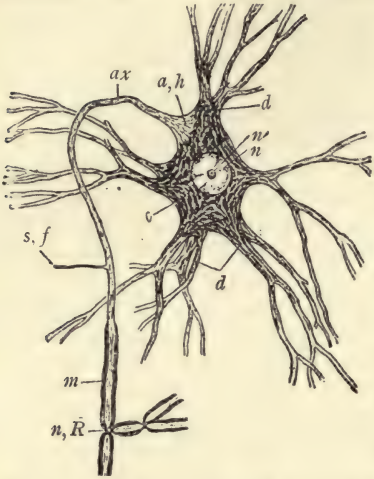


FIG. 127.—STRUCTURE OF MULTIPOLAR CELL (BARKER).

ah., Axon-hillock (the portion of the cell from which the axon comes off), containing no Nissl bodies, and showing fibrillation; *ax*, axis cylinder or axon; *m*, medullary sheath, outside of which is the neurilemma; *c*, cell-substance (cytoplasm), showing Nissl bodies in a lighter ground substance; *d*, protoplasmic processes or dendrites containing Nissl bodies; *n*, nerve-cell body or *perikaryon*; *n'*, nucleolus; *nR.*, node of Ranvier; *s.f.*, collateral fibril.

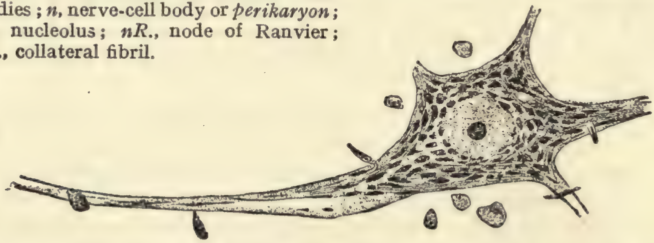


FIG. 128.—CELL FROM THE NUCLEI OF THE OCULO-MOTOR NERVE OF THE CAT (BARKER, AFTER FLATAU).

The nucleus, nucleolus, and Nissl bodies are shown on a larger scale than in Fig. 127.

neuro-fibrils previously spoken of. These pass from the dendrites of the cell into the cell-body, and from the cell-body they pass into the axon. The axon is therefore merely a bundle of neuro-fibrils, a nerve is the immensely elongated process of a nerve-cell. Cells with these processes vary in type and arrangement, but may be classified into the two groups previously mentioned of bipolar and multipolar. **Bipolar cells** are found typically in the ganglia on the roots of the spinal and cranial nerves. These cells are peculiar, inasmuch as they possess no dendrite process. The axon issues as a single process from the cell, and then divides **T**-shaped into two fibres (see Fig. 130); such cells would have been called one-poled, but for the fact that they are known by embryological studies to be bipolar. This type of cell is especially associated with the sensory nerves, and the axon is accordingly long, and may extend, say, from the foot to the spinal cord. The **multipolar cells** (Plate I., 3, and Fig. 129) are more widely distributed, and are found in the grey matter of the brain and spinal cord. They are furnished with processes and the usual axon, but the axon may be long or short, and this peculiarity enables multipolar cells to be divided into two groups, known as Golgi cells of the first and second type. Golgi cells of the first type may have an actual or relatively long axis cylinder. It may be a cylinder reaching from the cerebrum to the medulla, which would be relatively long, or from a segment of

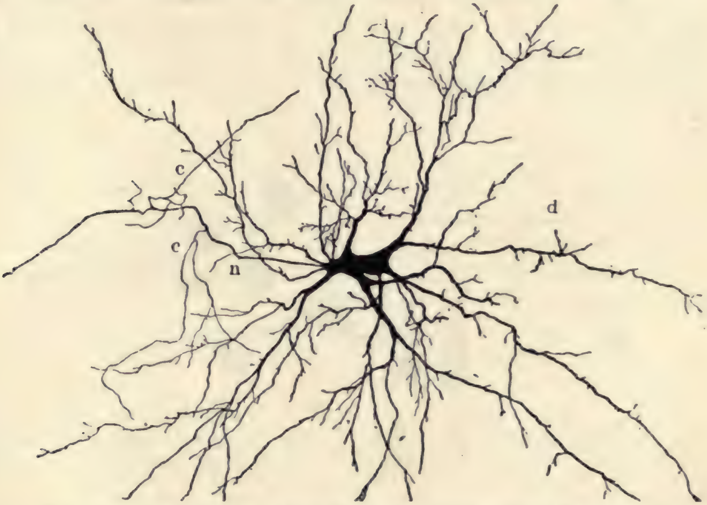


FIG. 129.—MULTIPOLAR NERVE-CELL (BARKER, AFTER KÖLLIKER).
n, Axon; *c c*, collaterals; *d*, dendrites.

the spinal cord to the foot, which would be actually long. This type of cell is associated with motor nerves. Golgi cells of the second type possess a short, widely-branched axon ; the axon never leaves the grey matter, and this type of cell may be seen in the cerebrum and cerebellum. Their short, widely-branching axons lead to the belief that such cells are distributive in function.

The processes leading to a cell are called **dendrites** (Fig. 129). Some cells, like the bipolar, have no such processes ; the multipolar, on the other hand, may be richly endowed. The neuro-fibrils found in the cell extend into it from the dendrites. The function of the dendrites is to collect impulses for transmission to the cell. The other process belonging to a cell is termed the **axon** (Figs. 127 and 129) ; it is the process which gives origin to the nerve-fibre, and into its substance the neuro-fibrils from the cell-body pass. Before the axon of a nerve becomes a nerve-fibre it gives off slender branches known as **collaterals** (Fig. 129) ; they may be few in number or numerous, as in the case of Golgi cells of the second type. A nerve-fibre terminates by ending in a fine tuft of branches in the neighbourhood of another cell ; the tuft is termed *arborisation*, and the junction thus formed with the neighbouring cell is termed a **synapse** (Fig. 132). It is believed that in the neighbourhood of synapses a receptive substance possessed of certain physiological properties exists which favours the transmission of impulses to the neighbouring cell, with which, it will be observed, it does not come into actual contact.

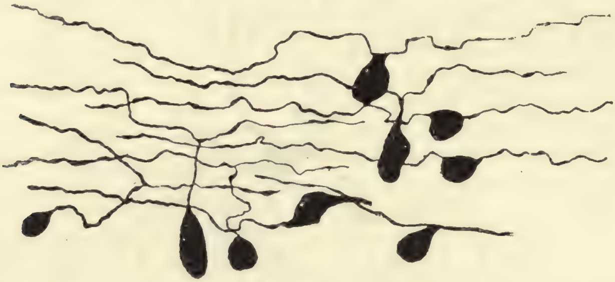


FIG. 130.

Cells from the Gasserian ganglion of a developing guinea-pig. The originally bipolar cells are seen changing into cells apparently unipolar. The same process occurs in the cells of the spinal ganglia (Van Gehuchten).

A nerve-cell, with its dendrites, axon, collaterals, and synapse, constitute a neurone. A **neurone** is a nervous system in miniature ; millions of such placed end to end, like the links in a chain, and side by side, like a series of chains, enable the nervous system to be visualised. Some of the links are short, others, we have seen, are long, but no link—viz., no single neurone—runs from the brain to the end of the body. The majority of the neurones originating in the brain are no longer than the nearest cell station, such as the basal ganglia and medulla ; as a rule, either in one or the other, or in both, of these places the neurone ends by arborising around a cell in a ganglion, and a fresh neurone is formed. Even when it gets into the cord it has not necessarily a long run ; it may run the length, but the majority of the cord neurones do not ; they dip into the grey matter at intervals, and arborise around cells from which fresh fibres arise. This may be the last cell station or not ; if it is the last, the axon passes out into a peripheral nerve, but even when outside the spinal cord a fresh break may occur—as we shall see in dealing with the sympathetic system—more arborising around cells in the sympathetic ganglia, and finally new fibres. This is what is meant in speaking of the neurones being arranged end to end like the links of a chain. In the simplest conceivable form of nervous mechanism the smallest number of neurones is two ; it is seldom that any such simple number exists in the body mechanisms ; as a rule, there are several breaks between the periphery and the brain, or the brain and the periphery. A single motor cell in the cerebrum, with its axon, is not connected with a single spinal motor neurone ; the latter may be connected with many such cerebral neurones. The sum of all the fibres in the white substance of the brain is, therefore, obviously larger than the sum of those in the cord.

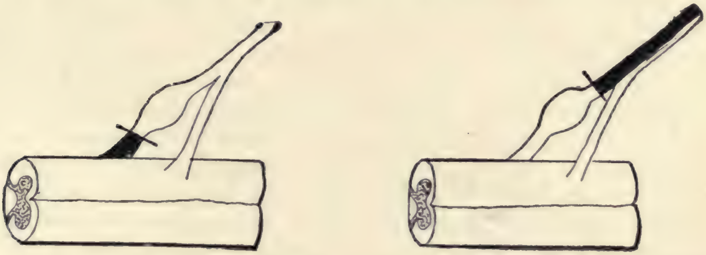
The conducting path is always from dendrites to cell, and from cell to axon. In a neurone a stimulus can only be transmitted in one direction—viz., from dendrite to axon, so that the dendrite is the receiving portion of the cell, the axon the issuing or distributing portion. No matter how many neurones the impulse has to pass through, nothing is lost excepting time. It is delayed, but it is carried from the termination of the axon across unoccupied fields to the nearest dendrites, and so transmitted to the next cell. There is no *contact* of the cellular elements of one axon with those of another. This is an essential part of the neurone doctrine. There is contiguity, but no structural continuity.

Such is the principle existing everywhere in the nervous system, brain or spinal cord, afferent or efferent nerves, cerebrospinal or sympathetic. There may be variations, and here and there the general rules of construction may be slightly departed from, but the principle is maintained—a principle which explains not only the anatomical but the physiological side of the system, and enables the mind to grasp a scheme of unity of construction throughout the entire nervous system.

The cell is the life of the fibre. If the fibre be cut off from the cell, it degenerates. Nor is the nutritional change confined to the fibre. The cell also suffers in consequence of loss of function, there being no impulses transmitted to it by its dendrites. The neurone concept consists in regarding the nerve-cell, its dendrites, its collaterals, axon, and terminal arborisation as a physiological unit. Innumerable such units, never touching, but yet brought closely together, constitute the nervous system.

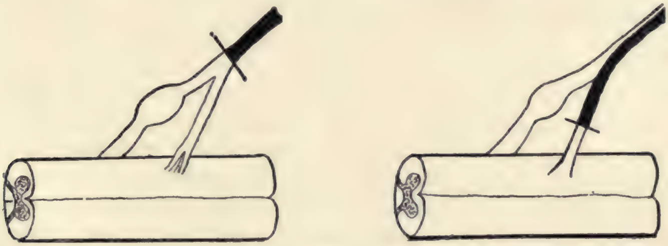
Degeneration and Regeneration of Nerves.—The cell nourishes the axon ; if, therefore, the axon be cut off from its cell, degeneration occurs, and this law applies to all cells cut off from their nucleus. We shall see presently that the great inflow and outflow of nerves from the spinal cord is divided into groups—afferent and efferent—broadly speaking, sensory and motor. Every axis cylinder is a nerve, and has a cell-station. In the case of the sensory nerves the cell-station is the ganglion or its root just outside the spinal canal ; in the case of the motor fibres the cell-station is in the ventral course of the grey matter of the cord. If a spinal sensory nerve be divided below the ganglion, the whole length of nerve below the ganglion, being cut off from its cell-station, degenerates. If the nerve be divided above the ganglion, those fibres which enter the cord from the **T** division of the two-poled cell alone degenerate, for it is only these which are affected by division above the ganglion (Fig. 131, 1). If the efferent or motor roots be divided, the cell-station being then above the division—viz., in the grey matter of the cord—the nerve degenerates downwards (Fig. 131, 4). If both roots of the spinal nerves be divided below the level of the spinal ganglion, both nerves degenerate in a downward direction (Fig. 131, 3). These profoundly interesting facts, discovered many years ago by the late Dr. Waller, are known after him as **Wallerian degeneration.** By this method of observation it became possible to trace the afferent paths in the spinal cord in consequence of the degeneration produced when these were divided above the ganglion.

The nerve-fibre, as has been stated above, is but a branch of a nerve-cell. If a portion of a cell be separated from the part containing its nucleus, it soon dies. Thus, when a large amœba, or a Radiolarian, is torn up into several pieces, the portions containing no nucleus degenerate and die ; but that portion containing the nucleus repairs itself and re-forms a perfect cell. The nerve-fibre dies down after being cut, just in so far as it is a piece of cell cut off from its nucleus. The sensory nerve divided in neurectomy, as practised on the horse, degenerates towards the foot, and not up the limb, for it is the piece below the wound which is cut off from its nutrient centre, and not the portion above. Had this been a motor nerve, the degeneration would still have taken place below the wound, and for the same reason. All spinal nerves have their seat of nutrition either in the spinal cord or in the ganglia just outside it. The nearer to the spinal cord the point at which the section is made, the greater the length of nerve which degenerates ; the further away from the cord the point at which section is practised, the shorter the length which degenerates. When the nerve degenerates, the fatty medullary sheath breaks up, forming globules around the axis cylinder. The latter also degenerates, and ultimately breaks up. The remarkable fact about these changes is the rapidity with which they occur, especially in the dog. Four days is sufficient to show their commencement. Small nerve-fibres degenerate more quickly than large.



No. 1.—Degeneration of afferent fibres caused by a section of superior root above the ganglion.

No. 2.—Degeneration of afferent fibres following a section of superior root below the ganglion.



No. 3.—Degeneration of efferent and afferent fibres following a section of the entire nerve.

No. 4.—Degeneration of efferent fibres following a section of inferior root.

FIG. 131.—DIAGRAMS TO ILLUSTRATE WALLERIAN DEGENERATION OF NERVE ROOTS (WALLER).

The microscopical changes in degeneration are very characteristic. In medullated nerves the axis cylinder swells and breaks up, and the medullary sheath disintegrates into droplets of myelin. Each detached piece of these undergoes a similar change, until the nerve is represented by a bundle of connective tissue without axis cylinder or medullary sheath, and the latter is abnormally filled with nuclei, the result of the proliferation of nuclei of the nerve (Fig. 124, II and III). In non-medullated nerve degeneration is represented by the disappearance of the axis cylinder. The nerve above the seat of division, though still in communication with the cell, undergoes a limited degeneration as the result of injury, and even the nerve-cells which are intact undergo temporary atrophic changes in consequence of their axons having been cut.

By suturing divided nerves union occurs, and though the act of division causes degeneration, yet, when union takes place, regeneration of fibres occurs. A fresh axis cylinder grows through the length of the degenerated nerve, and after some weeks, and often months, motion or sensation is perfectly or imperfectly restored. Sensation is always much later in appearing than motion. Even suture of divided nerves is not always necessary for union. It is known clinically that the plantar nerves of the horse will often unite in a few months, in spite of a piece being excised, the portion of nerve above sending down an axis cylinder, which soon finds out its divided portion below. If the gap between the divided ends of a nerve is considerable, a new axis cylinder cannot find its way across.

Trophic Nerves.—Not only is the nutrition of the nerve itself affected by nerve division, but also the nutrition of those parts supplied by it. Ulceration more or less severe has been known to follow injury of certain nerves. Sloughing of the cornea occurs in animals when the ophthalmic division of the fifth is divided, though this may be due to other causes than loss of trophic influence; and many are practically acquainted with the sloughing of the entire foot which sometimes, though fortunately rarely, follows the operation of neurectomy. It appears that nerves influence the nutrition of a part. It is well demonstrated in cases of intense muscular atrophy due to nerve injury, and in the dry papillated condition of the nose of the dog after division of the cervical sympathetic. The existence of special trophic nerves has been denied—*i.e.*, of nerves exclusively devoted to maintaining the nutrition of the part. Sloughing of the hoof a few days after neurectomy is evidence of the existence of some special nutrition having been cut off through division of the afferent fibres. The rapid degeneration of muscle after nerve injury is also suggestive of special trophic nerves; but, as the matter is still in dispute, no positive statement can at present be made.

SECTION 2.

Reflex Action.

Nerve-fibres do not under natural circumstances generate impulses; they transmit them, but without modifying them. Modification can only occur in nerve centres, such as the brain and spinal cord, and these centres always consist largely of nerve-cells, of which, as we have seen, the nerve-fibres leaving or entering the centre are simply processes or branches. The spinal cord may be described, not as one long centre, but a series of centres lying end to end, each capable to a greater or less extent of acting independently of its neighbour, and each centre possessing its afferent and efferent roots.

In these segments of spinal cord complex acts can be initiated by the arrival of simple afferent impulses. Such acts may be carried out without any assistance from the brain, for they can readily be demonstrated in an animal where the brain has been destroyed. These acts are known by the name of '**reflex,**' from which it must not be inferred that an afferent impulse is simply reflected into an efferent channel, but rather that an afferent impulse reaches the cord, and, passing into the grey matter, stimulates the ganglionic cells which generate the efferent impulse. The structures necessary for a simple reflex act are—(1) an afferent nerve to convey the impression to a nerve centre; (2) a nerve centre in which the outgoing impulses are generated; (3) an efferent channel for their transmission (Fig. 132). More complex acts may need more afferent nerves, a larger number of excitable centres, and a greater number of efferent fibres. The nervous chain is known as a **Reflex Arc,** and can never consist of less than two neurones.

A classical example of a reflex act is exhibited when a frog from which the brain has been entirely removed draws up its leg when the foot is pinched. Depending upon the degree of pressure applied to the foot, it draws up either one leg or both—*i.e.*, the reflex movements are unilateral or symmetrical, according to the number of ganglionic centres in the cord which have been stimulated. Still greater violence applied to the foot of this brainless frog will affect a larger number of centres further forward in the cord, so that the fore-limbs may share in the reflex. The brainless frog reacts more regularly to this experiment than one possessing a brain, which is evidence that the brain is capable of exercising a controlling influence or inhibitory effect over reflex actions. One very prominent feature of a reflex act is its apparently purposeful character. An opportunity for studying this in detail will be given presently when the 'reflex frog' is considered.

In the dog very characteristic reflex actions occur after division of the cord, such as those of walking, running, scratching, micturition, and defæcation; and some of these will shortly be considered in detail, owing to their deep physiological importance. The higher the animal scale is ascended, the less easy is it to obtain evidence of free spinal reflexes—viz., reflexes which take place without any guidance from the brain. This may perhaps be due to a more constant influence exercised over them by the brain. Nevertheless, animals as highly developed as the horse and ox give the most undoubted evidence of reflex spinal acts. If the spinal cord of either be severed behind the medulla, a cut

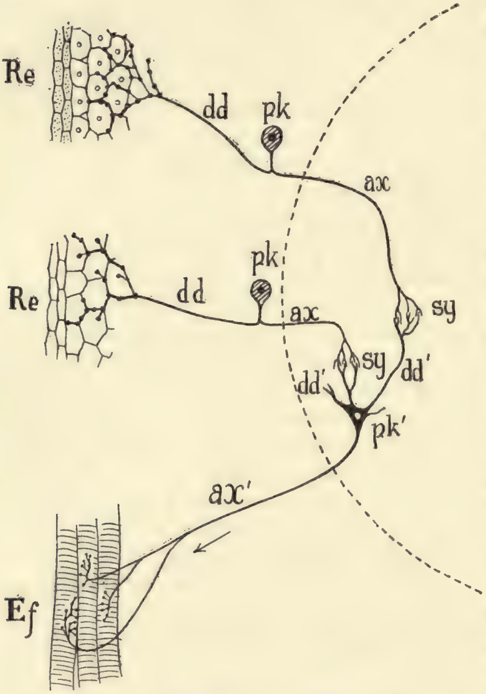


FIG. 132.—DIAGRAM OF A REFLEX ARC (SHERRINGTON).

The parts within the dotted line lie within the grey matter of the nerve centre.
Re, Re, Receptive surface, in this case the skin, impressions from which are conducted by afferent fibres, *dd, ax,* to a nerve centre, *pk'*, where outgoing impulses are generated; these are conducted by an efferent channel, *ax'*, to a discharging body, *Ef*, in this case muscle.
The figure is also employed to illustrate conduction and transmission of impulses along a nerve arc. The dotted line encircles a nerve centre (in this case the spinal cord). *dd* then become dendrites on their way to the perikaryon (see note, p. 433), *pk* (in this case the ganglion on the dorsal root of the spinal nerve), or if the perikaryon be short-circuited, the impulse passes direct to the axon, *ax*; this constitutes the *neuronic path*. *sy, sy* are synapses, by which the impulse is conducted to the next neurone, through the medium of dendrites, *dd', dd'*, and thence to *pk'*, the cell-body or perikaryon; this constitutes the *synaptic path*.

on the skin of the abdomen will evoke a kick. The excitability of the cord lasts for a few minutes after death; in the ox it lasts longer, but no comparative observations have as yet been made.

Locomotion is often essentially a reflex act. The exact grouping of muscles, and the regulation of the degree and rapidity of their contraction, would appear at first sight to need the supervision of the highest centres in the brain; but this is not the case. A pigeon will fly after decapitation; a brainless dog can walk, and a headless cat, under appropriate stimulation, flexes and extends its legs alternately. If a horse thought of every step he had to take, he would soon be worn out and blunder. That the higher centres also come into play is shown by the judgment which the animal exercises when jumping—viz., the proper distance at which to take off, the amount of muscular contraction required to lift the body, and the needful height to which it should be raised. Locomotion, however, is not purely a reflex act, as it is carried out with the knowledge and consent of the animal, but it functions as such. A true reflex act is involuntary, and carried out without the knowledge of the animal.

By a **Co-ordinate Movement** is meant one in which the contraction of various related groups of muscles is so adjusted that the extent of their contraction, and everything necessary for a perfect movement, is present and faithfully carried out. Co-ordination of movement may occur without the assistance of the brain. In the spinal cord, therefore, not only reflex but co-ordinate movements are generated. The crossed or diagonal movements of locomotion in quadrupeds are of this nature, and are carried out by the spinal cord. Movements which are irregular and purposeless, or in any way fail to co-ordinate, are termed **inco-ordinate.** We shall see later that the co-ordination of muscles is a complex reflex mechanism. All reflex actions are co-ordinate.

The Reflex Frog.—It is usual to illustrate reflex action by reference to the decerebrated frog. In this animal the spinal cord is capable of carrying out the most complex reflex acts, far higher in character than is exhibited by animals with a greater nervous development. If a decerebrated frog be placed in water, it swims; if it be stroked, it croaks; if stimulated, it springs; if placed on its back, it recovers its normal position; if acid be applied to the right thigh, the left foot will be employed to wipe it off; or if this be held, the right leg is flexed. Still more remarkable is the fact that if a decerebrated frog be placed on a board which is gradually brought from the horizontal to the vertical position, the animal gradually crawls up and, when the board is vertical, sits at the top. If the board be lowered to the opposite side, the creature descends. It is beyond the belief of a layman that such acts are not of a purposive character. As a matter of fact, they fall within the definition of a true reflex act.

If a headless frog be lightly stimulated on one hind-leg, a reflex contraction of the limb occurs ; if the stimulus is made stronger, both limbs react. By increasing the strength of the stimulus the fore-limbs may be involved, so that there is a proportion between the magnitude of the reflex acts produced and the strength of the stimulus. There is a latent period in a reflex act (see p. 459), and with each successive increase in the strength of the stimulus the latent period becomes longer in consequence of a greater length of cord being involved. If the frog be injected with strychnine and stimulated, convulsive movements occur, the sensitiveness to touch is greatly increased, so that even a current of air will cause muscular contraction. In this case it is supposed that there is an overflow, as it were, into all motor paths, the strychnine breaking down the usual barriers which direct the impulse. The strychnine does not open new paths, it uses the old ones, but it converts inhibitory effects into excitatory, so that contractions appear in muscles at the moment they should under normal conditions relax. Incidentally, the sensitiveness of the strychnine preparation demonstrates that a sensory path leads to all the motor neurones of the body.

The inhibition of reflexes is an extremely important question, which will receive separate consideration.

The reflex acts exhibited by the higher animals are more complex than those of the lower. The normal actions of the latter are almost entirely reflex, whereas those of the former are normally reflexes controlled, modified, or set free, as the case may be, by cerebral centres. If in the dog the cord be divided in the anterior thoracic region, the animal becomes paralysed, there is loss of sensation as well as of motion ; yet in process of time recovery occurs, and the isolated portion of cord is capable of carrying on the reflex function of micturition, defæcation, impregnation, parturition, scratching, and stepping, without the knowledge of the animal. Such a dog may even be able in course of time to walk or run. In the first instance it learns to stand, then takes a few steps before subsiding, and gradually the reflex paths are educated to the new condition which has arisen. Locomotion, we have stated, is not normally a true reflex act, yet under purely reflex conditions it may be carried out for hours. The horse has not to think of the order in which he uses his four legs, and how each step is to be taken ; the fact is that this is carried out by the spinal cord, with which the animal is not concerned ; the work is done for him.

It is only where judgment is required or instructions to be issued that the higher centres take any share in locomotion.

There are movements which may be excited in the limbs after death in both horse and ox, but particularly the latter, which remind one very strongly of the reflex frog. If immediately after a horse is destroyed an attempt be made to open the abdomen the animal kicks. Some minutes must be allowed to elapse before the irritability of the cord disappears. In the ox the period is longer, and even after decapitation the apparently purposeful movements are very remarkable. For these reasons we believe the cord plays in these animals a more independent part in locomotion than is generally considered. How largely locomotion is reflex may be indicated by the walking of the chick out of the egg. A volitional act requires some experience and training ; a reflex act is innate, and may be complete at birth.

Impulse Paths.—When an impulse enters the cord—and it can only gain entrance by the dorsal spinal roots—it may be dealt with locally by a single spinal segment. It may be distributed by several local segments, or it may pass the entire length of the cord and be dealt with by the cerebellum or cerebrum (Fig. 139, A and B). The strength of the entering stimulus may determine whether one or more segments of the cord is involved, as we have seen in the strychnine experiments on the reflex frog. Such a spreading of impulses is termed *irradiation*, and at one time it was believed that this could only occur in a forward direction. Sherrington showed that it could also occur down the cord, though it remains limited to certain lines. We may here trace the path of an impulse, selecting any spinal reflex act. What is true for this is true for all impulses passing to the cord by afferent nerves, and the principle is equally true for those, like sight, hearing, etc., which do not communicate with the cord, but pass direct to the brain. We have seen that a reflex arc (Fig. 132) consists of a chain of nerve-cells, each complete link being called a ' neurone,' and the neurones following each other end to end like the links of a chain. Further, that a complete neurone is made up of a nerve-cell body (perikaryon*) with its processes, some of these, the dendrites, being the receiving, another the axon, being the transmitting process. We also know that the axon terminates by arborising around the dendrites of the next link. The passage of an impulse in a nerve-arc must lie during part of its course, within the neurone (in all cases travelling from dendrite to axon, though not necessarily traversing the perikaryon, which may be short-circuited). Having arrived at the end of one neurone, the impulse has then to cross the space existing between it and its neighbouring neurone ; the region in which this occurs is the synapse. Conduction is therefore in part *within* the neurone, or intraneuronic, shortly *neuronic*, and in part *between* the neurones, interneuronic, or preferably *synaptic*, as it occurs in the area of a synapse (Fig. 132). The whole of the conduction and transmission of impulses in the nervous system then become describable as (1) neuronic and (2) synaptic, and this distinction is physiologically fundamental because the nature of the conduction cannot be the same in the two cases. In all nerve-centres synaptic conduction is added to neuronic conduction ; synaptic conduction is irreversible in direction, neuronic conduction is reversible.

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* See footnote, p. 433.

The **Receptor System** has been revealed by the work of Sherrington ; it is a system engaged in the transmission of impulses from the periphery to the centre, which result in a reflex act. It forms the basis of the classification of afferent nerves on p. 422. The impulses are received in what he has termed 'fields of distribution,' and of these there are two main divisions—*surface* and *deep*. A surface field may be external, or *exteroceptive*, such as the skin, or an internal surface field (*interoceptive*), such as the mucous membrane of the nostrils. The deep field, or *proprioceptive* system, lies in the muscles, joints, tendons, viscera, etc. Whereas the surface field is brought into operation by its surroundings, such as touch, pressure, heat, cold, sight, hearing, smell, the deep field is activated by something derived from itself ; for example, mass, weight, pressure or alteration of pressure, such as occur in a contracting or relaxing muscle. The first step, then, in the conveyance of an impulse—say, from the skin to the cord—is that the nerve path shall originate in a *receptive field*. An area of skin consists of points forming a receptive surface, from which the nerve path starts. The receptive neurone extends from the receptive surface to the central nervous organ, and it forms the sole avenue which impulses generated at its receptive point may use, no matter whither they may be proceeding or how distant their destination.

A single receptive point may play reflexly upon a number of different effector organs—*i.e.*, organs connected with the efferent system, muscles, glands, and suchlike—yet all its reflex arcs spring from the one single shank—viz., from one afferent neurone, which conducts from the receptive point at the periphery into the central nervous organ. This neurone dips at its deep end into the spinal cord or brain, and in this network forms manifold connections. So numerous are its potential connections that, as shown by the general convulsions induced under strychnine-poisoning, its impulses can discharge every muscle and effector organ in the body. Yet under normal circumstances the impulses conducted to the central network do not irradiate in all directions. Their spread, as judged by the effects, increases with increase of stimulation of the radiant path, but the irradiation remains limited to certain lines. Under weak stimulation these lines are few. The conducting network affords, therefore, to any given path entering it, some communications that are easier than others. This is sometimes expressed, borrowing electrical terminology, by saying that the conductive network from any given point offers less resistance along certain circuits than along others. This recognises the fact that the conducting paths in the great central organ are arranged in a particular pattern. This pattern of arrangement of the conducting network of the central organ reveals something of the integrative function of the nervous system. It tells us what organs work together in true relationship. The impulses are led to this and that effector organ, gland, or muscle, in accordance with the pattern.

The receptive neurone forms, as we have seen, the sole avenue by which impulses generated at its receptive point can be conveyed to their destination. It is a path exclusive to the impulses generated at its own receptive points, and other receptive points than its own cannot employ it. The receptive neurone forms a **private path** exclusively devoted to impulses from a single receptive point. Our study of the skin will have shown that its entire surface is a collection of receptive points. On reaching the cord the impulses pass along certain *association*-tracts or *internuncial* paths—*i.e.*, paths which connect the various segments of the cord. These are paths common to groups of private paths, and at their termination the impulses pass from their synapses across the space which separates them from the first link or neurone in the chain of the efferent path. The efferent path passes out in the case of the cord, by the inferior spinal nerves to the gland or muscle concerned, where it terminates in a final neurone. The motor or efferent path differs in one important respect from the sensory or afferent, inasmuch as it is not exclusively devoted to the transmission of impulses generated at one single receptive source alone, but receives impulses from many receptive sources situated in various regions of the body. It is the sole path by which all impulses, no matter whence they come, must travel if they would reach the muscle, gland, etc., concerned. It is a **public path** common to impulses of all kinds, such as tissues are constantly receiving. Reflex arcs arising, therefore, in different sense-organs can pour their influence into one and the same muscle. A limb-muscle is the *terminus ad quem* of nervous arcs arising not only in the right eye, but in the left ; not only in the eyes, but in the organs of smell and hearing ; not only in these, but in the otic labyrinth, in the skin, and in the muscles and joints of the limb itself, and of all the other limbs as well. Its motor path is a nerve common to all these. It is the **final common path,** and a motor nerve to a muscle is a collection of such final common paths.

The afferent neurones comprising the private paths are several times more numerous than the common paths ; in other words, the outlet is much smaller than the inlet, and in consequence there is competition for the right of way. In this matter there is no compromise in a conflict, say, between two opposite reflexes. One or the other must pass, both cannot. We shall see this well illustrated in the 'scratch' and 'foot reflex' of the dog. The victory in this struggle lies, as usual, on the side of big battalions. The stronger the stimulus, the more likely is it to occupy the road, especially if it be of a painful nature. The stronger inhibits the weaker. The weaker is not necessarily destroyed ; it may simply be held back, and permitted to follow when the stronger rival has left the road open. Inhibition does not take place in the motor nerve itself. The field of competition between the rival arcs seems to lie in the grey matter, where the converging neurones come together at the commencement of the common path, and here it is that some arcs drive the final path into one kind of action ; others drive it into a different kind of action ; and others, again, preclude it from being activated by the rest. In studying the reflex act of stepping, this feature will be well illustrated in the reciprocal innervation of antagonistic muscles. We have previously learnt (p. 402) that while the flexor muscles of a limb are contracting the tone of the extensor muscles is inhibited ; this inhibition arises in the nerve-centre, the stream of motor impulses along the motor neurone being for the time cut off in the struggle for the common path. This fact is of the utmost importance to a clear understanding of the question of muscular co-ordination, and further consideration of the question will occur later.

On the receptive surface the various impressions, such as light, touch, heat, cold, and so forth, are picked out by the special afferent nerves devoted to their transmission. The spinal connection of different nerve-endings in the same area of skin is assumed to be different, since stimuli suitable for one set of movements are unsuitable for another. The scratch reflex needs tickling or stimulation of a hair for its production. The reflex of the 'extensor thrust,' which has yet to be spoken of, can only be excited by pressing between the plantar cushion and the toe-pads of the dog, and no other form of stimulation can invoke it. A consideration of the special spinal reflexes now to be described will prove object-lessons in the principles of the common path, and the remarkable mechanisms it is capable of effecting.

The Stepping Reflex.—When in the dog the spinal cord has been severed in the hinder part of the cervical region, and the 'shock' from the transection has passed off, reflex walking is observable. The walking movement includes alternate flexing and straightening of the limb. The forward movement of the hind-leg in taking a step is produced by flexion at the hip, and to prevent the foot brushing against the ground as the leg swings forward flexion occurs at the stifle and hock, so as to somewhat raise the foot. The limb is then straightened again, so that the foot may reach the ground and bear the weight of the body. In order to prevent the limb doubling up under this burden, the extensor muscles which support the patella joint and hock from bending have to contract with sufficient power. Stiffened by the contraction of these muscles, the limb serves as a prop to carry the body. While the foot rests on the ground the body moves forward, so that in due course the hip advances in front of a vertical drawn upward from the foot. The extended hind-limb at this time is sloped somewhat backward as well as downward. When this posture is reached, the extensor muscles are thrown into further action, and give the limb a push off from the ground, propelling the body forward. The hind-limb thus makes its contribution to the forward progression of the body; in galloping in the normal dog this extensor thrust is very marked.

In this reflex spinal stepping, we may study first the flexion of the limb which occurs in the forward movement of the step. Flexion similar but more pronounced can be easily excited in the *spinal dog** by exciting the skin of the foot electrically. Though the flexion occurs at hip, patella joint, and hock together, it will be simpler to confine our examination to the flexion at one of these joints only, for what occurs in the muscles of each of the three joints is, so far as concerns us now, the same. The chief muscles which flex the stifle are the *semitendinosus* and *biceps* of the back of the thigh. The electric stimulation of the skin of the foot is found to throw these muscles into contraction, and, with them, also the *psoas* muscles (flexors of the hip) and the *tibialis anticus*, etc. (flexors of the hock). But this is only part of what happens. At the same time as the flexors of the stifle contract, the extensor muscles of the stifle, the *vasti* and *crureus*, are relaxed. The same stimulus which excites the motor neurones of the flexors to discharge motor impulses into those muscles, causes the motor neurones of the antagonistic muscles, the extensors of the knee, to cease discharging impulses, and keeps them prevented from discharging impulses. The stimulus sets up an intraspinal *excitation* of the motor neurones of the flexor muscles and an *intraspinal inhibition* of the motor neurones innervating the extensor muscles.

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* 'Spinal dog' is the term used to indicate that the reflexes are entirely spinal, owing to the brain having been destroyed, or the cord having been cut off from the brain.

When the flexion phase of the act of stepping has been passed through, the leg extends again by return of activity in the motor neurones of the extensor muscles which had been inhibited. In due course the foot reaches the ground. When it does so the weight of the body gradually comes upon it, and soon presses the sole of the foot with its full force against the ground. A stimulus is thus given to nerve-endings in the sole. This stimulus can be imitated—for instance, by pressing against the toe-pads with a finger. This, in the spinal dog, even when the animal is lying on its side, excites a strong reflex extension of the limb, the '**extensor thrust.**' Just such an extension occurs when the foot is pressed against the ground by the weight of the body in the act of stepping. This extensor thrust gives the propulsive movement of the body forward, which is the contribution made by the limb in its reflex step toward the progression of the animal. The extensor thrust is particularly marked in the gallop.

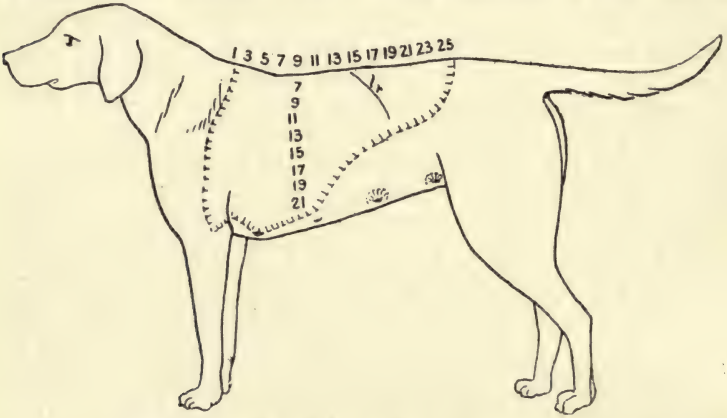

FIG. 133.—THE SCRATCH REFLEX (SHERRINGTON).

The 'receptive field,' as revealed after low cervical transection, a saddle-shaped area of dorsal skin, whence the scratch reflex of the left hind-limb can be evoked. *lr* marks the position of the last rib.

The Scratch Reflex.—Good opportunity for study of this correlation between reflexes is given in the 'scratch reflex.' This reflex can be easily elicited in many normal dogs; when the spinal cord has been transected in the neck, it becomes abnormally prominent. Stimuli applied within a large saddle-shaped field of skin (Fig. 133) excite a scratching movement of the leg. The movement is rhythmic flexion at hip, stifle, and hock. It has a frequency of about four per second. The stimuli provocative of it are mechanical, such as rubbing the skin, or pulling lightly on a hair. The nerve-endings which generate the reflex lie in the surface layer of the skin, about the roots of the hairs. A convenient way of exciting these is by feeble faradisation.

Prominent among the muscles active in this reflex are the flexors of the hip. If we record their rhythmic contraction we obtain tracings, as in Fig. 135. A series of brief contractions succeed one another at a certain rate, whose frequency is independent of that of the stimulation. The contractions are presumably brief tetani. The stimulus to the hair-bulbs of the shoulder throws into action a lumbar spinal centre, innervating the hip-flexor, much as the bulbar respiratory centre drives the spinal *phrenicus* centre. In the case of the respiratory muscle the frequency of the rhythm is, however, much less.

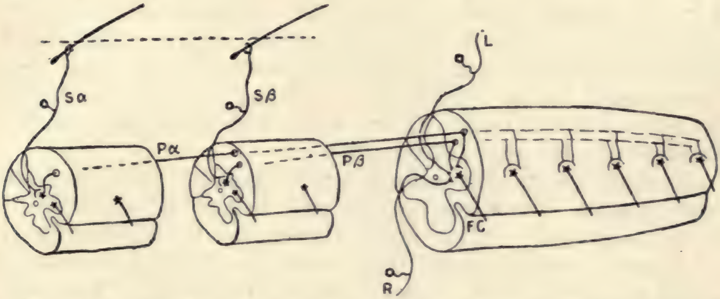

Fig. 134.—Spinal Arcs involved in Scratch Reflex (Sherrington).

Diagram of the spinal arcs involved in Fig. 133. L, Receptive or afferent nerve path from the left foot; R, receptive nerve path from the opposite foot; Sα, Sβ, receptive nerve paths from hairs in the dorsal skin of the left side; FC, the final common path, in this case the motor neurone (nerve path) to a flexor muscle of the hip; Pα, Pβ, neurones originating within the cord.

The reflex is unilateral: stimulation of the left side of the back evokes scratching by the left leg, not by the right. In the lateral column of the spinal cord fibres exist directly connecting the spinal segments of the shoulder with the spinal segments containing the motor neurones for the flexor muscles of the hip, and knee, and ankle. We thus arrive at the following reflex chain for the scratch reflex: (1) The receptive neurone (Fig. 134, Sα), from the skin to the spinal grey matter of the corresponding spinal segment in the shoulder. This is the exclusive or private path of the arc. (2) The long descending neurone within the cord (Fig. 134, Pα), from the shoulder segment to the grey matter of leg segments. (3) The motor neurone (Fig 134, FC), from the spinal segment of the leg to the flexor muscles. This last is the *final common path.* The chain thus consists of three neurones. It enters the grey matter twice—that is, it has two neuronic junctions, two synapses. It is a *disynaptic* arc.

Now if, while stimulation of the skin of the shoulder is evoking the scratch reflex, the skin of the hind-foot is stimulated, the scratching is arrested. Stimulation of the skin of the hind-foot causes the leg to be flexed, drawing the foot up. This is the **foot reflex.** The drawing up of the foot is effected by strong tonic contraction of the flexors of hock, stifle, and hip. In this reaction the reflex arc is: (1) The receptive neurone or nerve path (Fig. 134, L) from the foot to the spinal segment; (2) perhaps a short intraspinal neurone; and (3) the motor neurone or nerve path (Fig. 134, FC) to the flexor muscle—*e.g.*, of hip. Here, therefore, we have an arc which embouches into the same *final common path* as S*a*. The motor neurone FC is a nerve path common to it and to the scratch reflex arcs; both arcs employ the same effector organ, a hip-flexor.

The channels for both reflexes finally embouch upon the same common path. The flexor effect specific to each differs strikingly in the two cases. In the scratch reflex the flexor effect is an intermittent contraction of the muscle; in the foot reflex it is steady and maintained. The accompanying tracing (Fig. 135) shows the result of conflict between the two reflexes. The one reflex displaces the other from the common path. There is no compromise. The scratch reflex is set aside by that of the reflex arc provoked from the foot. The stimulation which previously sufficed to evoke the scratch reflex is no longer effective, though it is continued all the time. But when the stimulation of the foot is discontinued the scratch reflex returns. In that respect, although there is no enforced inactivity, there is *inhibition.* There is interference between the two reflexes, and the one is inhibited by the other. Though there is no cessation of activity in the motor neurone, one form of activity that was being impressed upon it is cut out and another takes its place.

Suppose, again, during the scratch reflex, stimuli are applied to the foot, not of the scratching, but of the opposite side (Fig. 134, R). This stimulation of the foot causes flexion of its own leg and extension of the opposite. If, when the left leg is executing the scratch reflex, the right foot is stimulated, the scratching, involving as it does the left leg's flexors, is cut short. This inhibition of the flexor scratching movement occurs sometimes when the contraction of the extensors is minimal or hardly perceptible.

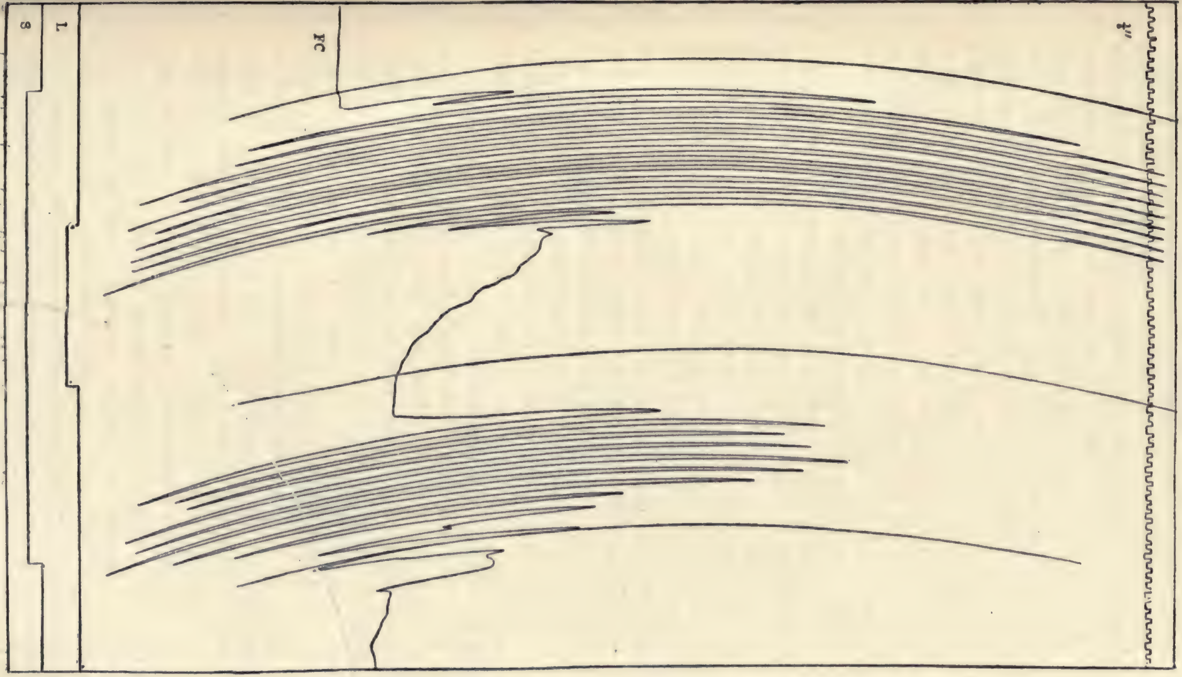

FIG. 135.—THE RESULT OF CONFLICT BETWEEN TWO REFLEXES.

Interference between the reflex action of the left hip-flexor, FC, caused by the nervous arc from the left foot (L, Fig. 134) and the scratch reflex. The stimulation of the dorsal skin (Fig. 134) inducing the scratch reflex began at the beginning of the notch in the signal line S, and continued throughout the period of that notch. Later, for the period marked by the notch in signal line L, the stimulation of the foot was made. This latter stimulation interrupts the clonic scratch reflex in the manner shown. The time is registered above in fifths of seconds. The tracing reads from left to right. It is noteworthy that the interruption of the scratch reflex by the foot reflex is not established directly the foot stimulus begins, and that it outlasts for a short time the application of the foot stimulus.

It is obvious from this that the final common path, FC, to the flexor muscle can be controlled by, in addition to the beforementioned arcs, others that actuate the extensor muscles, for it can be thrown out of action by them. The final path, FC, is therefore common to the reflex arcs, not only from the same side foot (Fig. 134, L) and shoulder skin (Sα, Sβ), but also to arcs from the opposite foot (R), in the sense that it is in the grasp of all of them. In this last case we have a conflict for the mastery of a common path, not, as in the previous instance, between two arcs, both of which use the path in a pressor manner, although differently, but between two arcs that, though both of them control the path, control it differently, one in a pressor manner heightening its activity, the other in a depressor manner lowering or suppressing its activity.

We said that the scratch reflex is unilateral. If the right shoulder be stimulated, the right hind-leg scratches ; if the left shoulder be stimulated, the left hind-leg scratches. If both shoulders be stimulated at the same time, one or the other leg scratches, but not the two together. The one reflex that takes place prevents the occurrence of the other. The reason is that, although the scratch reflex appears unilateral, it is not strictly so. Suppose the left shoulder stimulated. The left leg then scratches. If the right leg is then examined, it is found to present steady extension, with some abduction. This extension of the leg which accompanies the scratching movement of the opposite leg contributes to support the animal on three legs, while it scratches with the fourth.

Suppose now we stimulate the left shoulder, evoking the scratching movement of the left leg, and that the right shoulder is at the same time appropriately and strongly stimulated. This latter stimulus often inhibits the scratching movement in the opposite leg, and starts it in its own. In other words, the stimulus at the right shoulder not only sets the flexor muscles of the leg of its own side into scratching action, but it inhibits the flexor muscles of the opposite leg. It throws into contraction the extensor muscles of that leg. In the previous example there was a similar co-ordination. The motor nerve to the flexor muscle is therefore under the control not only of the arcs of the scratch reflex from the shoulder on the same side, but of those from the opposite shoulder as well. But in regard to their influence upon this final common path, the arcs from the homonymous shoulder and the opposite shoulder are opposed.

The scratch reflex occurs in many animals besides the dog—e.g., the cat, guinea-pig, sheep, rabbit, rat, parrot. In small animals its rate of rhythm is greater than in large ; the scratch is quicker in small dogs than in large.

Tendon Reflexes.—One of the best known of the tendon reflexes in man is the knee-jerk, a jerking forward of the leg when the straight ligament of the patella is struck. This is caused by a momentary single spasm of the extensor muscles of the knee, and although often called a reflex act, cannot truly be so, because the time between the blow and the jerk is too short for any reflex act. It is well seen in the dog, cat, rabbit, etc. Although not a reflex action, it is dependent on the reflex tonus that is maintained in the muscles by the spinal arcs connected with them ; if that tonus be much lowered, as by severance of the nervous reflex arc, the jerk can no longer be elicited. The jerk is a good index of the condition of the reflex arc, and therefore of the condition of the activity or depression of the segments of the cord by which the extensor muscles are innervated. It is depressed during sleep or anæsthesia, and by anæmia of the cord ; it is intensified when the cerebral restraint is removed from the lumbar spinal segments by diversion or attention to another part, or by severance of the cord in the dorsal region. Another brisk ' jerk ' in the dog is the ischial, obtained from the hamstring muscles by tapping the tuberosity of the ischium.

Tendon reflexes have not, so far as we are aware, been studied in the ungulates ; nor is it known whether the existence of any reflexes has been demonstrated, if, perhaps, we except the immediate lifting up of the foot, which generally follows pressure on the so-called ' chestnut ' found on the inside of the fore-arm of the horse.

Reflex Inhibition.—In the reflex movements of ' stepping ' and ' scratching ' in the spinal dog, attention has been drawn to acts of inhibition ; for instance, it was shown that the stimulus which excites the flexors to contract causes the extensors to relax. The stimulus to produce contraction in the extensors is still present, but it is inoperative, owing to inhibition. It was also shown that the scratch reflex, having been started on one side of the body, could be inhibited by starting it on the opposite side. In this case the stimulus starts one set of flexor muscles going, and inhibits the corresponding set of flexors in the opposite limb. Similarly, in the conflict between the two reflexes of scratching and stepping, all the conditions needful to maintain the scratch reflex in operation are present, but they are inhibited so long as the pad of the foot is pressed upon ; when that stimulation is withdrawn, the scratch reflex returns. We have therefore to consider the question of *reflex inhibition.*

The visceral muscles receive, as we have already seen, a double source of efferent nerve supply. The heart-muscle and that of the intestines and bloodvessels can be stimulated or inhibited ; this is effected by one efferent conveying impulses of an excitatory character, while the other efferent conveys inhibitory impulses. These work reflexly under the control of an afferent service, and the nature of the impulses in the afferent determine which of the efferent impulses are to be placed in operation. Muscles, as we have seen, are provided with an effective afferent system of nerves, more than half the fibres belonging to a muscle being of this nature. Sherrington has shown that where the muscle passes into the tendon, a 'nest of afferents' exists, and he has also proved that the Golgi organ found in tendon is afferent in nature. In spite of this liberal afferent system, there is only a limited efferent outflow; muscles are well supplied with nerves conveying excitatory (motor) impulses, but there are no nerves conveying inhibitory impulses. Notwithstanding, inhibitory functions in skeletal muscle are of a most important and widespread character, and they are effected in a purely reflex manner by inhibiting the neurone which conveys the excitatory impulses.

Under the title of **reciprocal innervation** Sherrington describes what occurs in all normal movement—*i.e.*, a relaxation of antagonistic muscles. For instance, while the flexors of a limb are contracting, their antagonists, the extensors, are relaxing. This effect is brought about by the tonus (p. 402) of the antagonistic muscles being reduced, owing to an inhibition of the motor cells in the cord which supply the extensor muscles. Reciprocal innervation also saves a waste of nervous energy in overcoming the contraction of antagonists, and it ensures muscular co-ordination. In certain muscular movements antagonistic muscles may contract concurrently. This is evident in those cases where a muscle is connected with two or more joints, being a flexor of one and an extensor of another. In this case antagonistic muscles are capable by their contraction of inhibiting the extensor movement of one joint in order to permit the muscle to act as flexor of another. The innervation of the antagonistic muscles so employed is no longer reciprocal, but identical, as they must contract and relax at the same time, and not alternately.

The purposes served by reflex inhibition in skeletal muscular actions are classified by Sherrington as follows :*

1. Reflex inhibition cuts short the contraction of one set of muscles when another set is called into play ; it also guards and maintains a reflex already in operation, by preventing its being interrupted by other stimuli.

2. It grades the degree of intensity of the discharge from nerve centres, by diminishing it to any required extent, so that the needful discharge from a motor centre can be adjusted with the greatest precision.

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* 'The Rôle of Reflex Inhibition,' *British Medical Journal*, March 25, 1911, and *Science Progress*, No. 20, April, 1911.

3. Reflex inhibition exhibits itself in respiration, stepping, eyeball movements, and the reciprocal innervation of antagonistic muscles, the underlying principle being that by means of reflex inhibition the contraction of a muscle causes relaxation of its antagonist.

4. Inhibition is the main means by which rhythmic reflexes are produced. For example, the rhythmic reflex in stepping being excited, its execution produces a stimulus, which brings into activity a reflex inhibition ; this cuts the rhythmic reflex short. The muscle having ceased to contract, the inhibition is removed, and the original stimulus is once more in undisputed possession of the field, and so rhythmicity is maintained.

5. On the withdrawal of inhibition, there is a great augmentation of activity in the inhibited centre. This Sherrington describes as **post-inhibitory rebound ;** this rebound favours the change from flexion to extension and *vice versa*. He regards it as responsible for one of the two phases of such diphasic muscular reflexes as stepping, mastication, and respiration. It is evident that when one or more pairs of legs are concerned in locomotion, some of the limbs are in a condition of flexion, the others are in extension ; and the change from one phase to the other is brought about by post-inhibitory rebound.

6. Strychnine converts reflex inhibition into *reflex excitation*, and the toxins of tetanus and rabies have the same effect. These agents, as pointed out by Sherrington, 'work havoc' with the elemental co-ordination of the skeletal muscles, changing reciprocal innervation into identical innervation. Hence, in tetanus patients, the greater the effort to open the jaw, the more tightly is it closed ; and in the hydrophobia patient the greater the attempt made by the sufferer to inhibit his inspiration in order to swallow, the deeper and more prolonged the inspiration which ensues, inhibition 'being converted by the virus into excitation.'

7. Chloroform and 'fatigue' strengthen inhibition. An inhibitory reflex stimulus which is ineffective on a normal centre, when that centre is fresh, becomes effective when the centre is under chloroform, or when the active driving of the centre has been pushed for a little time.

In complex reflexes many stimuli are at work together, and co-operate harmoniously for a co-ordinate result. In standing, walking, running, etc., very important sources of the reflex lie in the muscles and joints of proximal parts of the limb—namely, in the joints of the hip and stifle and the great muscles acting on them. These joints and muscles are liberally supplied with afferent nerves. The importance of these as sources of the reflex of stepping is indicated by several facts. In the first place, a dog or cat is found still to walk well when the foot reflex is cut off in all four feet by division of the nerves, both superficial and deep. In the second place, when the spinal dog is lifted so that its limbs do not touch any solid support whatever, reflex walking and galloping are performed, although the limbs are stepping wholly in the air. But to excite this reflex of walking in the air, it is necessary that the limbs hang down. The reflex ceases if the dog be inverted, when gravity no longer is acting on the joints and muscles as it does in the position usually accompanying acts of stepping. It is evident that impulses which stimulate contraction are passing from muscles and joints to spinal centres. The spinal centres which execute reflex walking, running, etc., receive much help and direction from afferent arcs which arise in the labyrinth of the ear. The stimuli, which are the source of reflex walking, etc., arise, therefore, in many receptive organs.

It is by means of the deep stimuli that the proprioceptors of the limbs maintain the extensor muscles in a state of tonic activity, and so enable the upright position of the body to be maintained without effort and without the knowledge of the individual. When, therefore, the spinal dog is held in the air legs downwards, gravity acting on the joints and muscles—viz., weight and pressure—is the cause of impulses passing from the deep fields to the spinal cord, and so maintaining the act of stepping. When the animal is inverted, the deep fields no longer receive their natural stimulus, and the movement ceases. We shall see shortly that the chief ganglion controlling the *proprioceptive system* is the cerebellum.

The Standing Reflex.—When the brain of a dog or cat is removed between the anterior and posterior *colliculi*, the extensor muscles of the limbs, the extensor muscles of the neck, back, and tail, and those which close the jaw, are in a condition of mild tonic contraction. Their antagonists, the flexors, exhibit relaxation. The phenomenon is known as **Decerebrate Rigidity.** The rigidity of the extensor muscles is due to impulses passing out from the cord as a reflex effect, for if the afferent nerves of the muscle be divided the rigidity ceases. The reflex effect originates in the muscle, for if the nerves of the skin be divided the rigidity continues. The decerebrate preparation if stood on its legs, remains there, the rigidity of the extensor muscles of the above-named parts sufficing to maintain the erect attitude, even for hours at a time. From the above experiment of Sherrington's it is evident that the standing posture is a reflex act, and he has further shown that the destruction of the labyrinth, either before or after decerebration, does not prevent rigidity of the extensor muscles occurring. When, however, the brain is divided behind the pons the preparation can no longer remain erect, nor can a decapitated dog or cat stand. The act of standing in the normal animal receives full consideration in a subsequent chapter on the Locomotor Apparatus.

Other Reflex Acts.—We have seen that reflex acts are not confined to those affecting skeletal muscles; the act may be a secretory or nutritive one, or involving the contraction or relaxation of pale muscle; for example, the contraction and dilatation of the bloodvessels under the influence of the vasomotor system, the peristaltic movements of the intestines, the contraction of the bladder and uterus, and the secretions from various glands, are all examples of reflex acts.

Reversal of Reflex Effect.—The influence of the nervous system in regulating the calibre of the bloodvessels as a reflex effect has been dealt with elsewhere (pp. 57, 58). It is not proposed to refer again to this, excepting to illustrate a phenomenon known as reversal of reflex effect. When an ordinary afferent nerve is stimulated in the dog, the effect produced on the bloodvessels is that of constriction, and the blood-pressure is reflexly raised. Bayliss has shown that a rise in pressure can be converted into a fall by a sufficient dose of chloroform. In observations by Sherrington and Sowton on skeletal muscle, it was found that the excitatory reflexes brought about by strychnine could be undone by chloroform or ether, so that the reflex response could be changed back from contraction to inhibitory relaxation, and on allowing the chloroform narcosis to partially pass off, the strychnine influence reappears. In the decerebrate preparation the above observers showed that reflex contraction of skeletal muscle or reflex inhibition could be produced at will through the same afferent nerve by varying the strength and form of the electrical stimulation, and in other ways. Instances begin to be numerous in which the reflex obtainable from one and the same afferent nerve may be diametrically reversed on alteration of some one definite factor in the conditions of the reaction.

Peripheral Reflex Centres—viz., centres for reflex action outside the brain and spinal cord—have long been carefully looked for, especially in connection with the sympathetic system. So far as is known, there are no purely sympathetic reflex acts ; nor are all the necessary physiological structures present in the sympathetic system for the formation of a reflex arc. The ganglia on the dorsal roots of the spinal nerves are similarly structured ; they are not seats of reflex action, and for the same reason. We have seen that a reflex arc requires a sensory nerve, a centre, and a motor nerve. All three of these are not present in connection with a sympathetic or spinal ganglion.

The **Time occupied by a Reflex Act** varies dependently upon the strength of the stimulus and the nature of the reflex ; the sharper the stimulus, the more immediate the reflex ; the more active the centre, the more rapid the response. Impulses which have to cross the cord take longer than those which enter and return from the same side. It is mainly during this appreciable delay, or latent period, as measured by delicate apparatus, that the changes are occurring in the grey substance which lead to an efferent response. In the dog the time occupied by a reflex on the same side is estimated at 0·022 up to 2-3 seconds, according to circumstances.

SECTION 3.

Spinal Cord.

The spinal cord extends from the atlas to about the second or third sacral vertebra, and is completely enclosed in a dense membrane, the dura mater. The canal in which it is lodged is very much larger than the cord, especially at those parts where the greatest amount of movement occurs, as in the neck. The cord is not the same shape nor the same size throughout; oval in the cervical region, it becomes circular in the dorsal, and again oval in the lumbar portion. It is largest where any considerable bulk of nerves is being given off, and thus there is an enlargement corresponding to the fore, and another to the hind limbs (Fig. 136). On exposing the spinal canal, a large number of nerves are found to be passing through the dura mater either outwards or inwards, and these gain an exit from or entrance to the spinal canal by means of the foramen formed at the junction of the vertebræ.

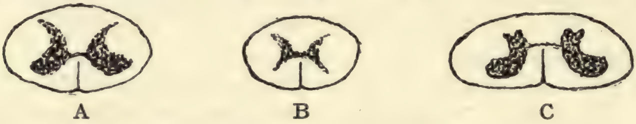

FIG. 136.—TRANSVERSE SECTION OF SPINAL CORD OF HORSE.

A, At level of first dorsal vertebra; B, at level of first lumbar vertebra; C, at level of first sacral vertebra.

Spinal Nerves.—These are given off from or enter the cord from the first bone of the neck to the fourth or fifth sacral vertebra. A bunch of nerves passes through every intervertebral foramen on each side, and this represents the spinal nerves. When the dura mater of the cord is opened, it is observed that the nerves, after entering this cover, divide into two groups: one passes to the dorsal, the other to the ventral, aspect of the cord. These are the superior and inferior roots of the spinal nerves, or, to maintain the preferable nomenclature, the dorsal and ventral roots. In the horse the dorsal and ventral roots enter the cord, not as a single bundle, but as several. On the dorsal root a nodule is found where the nerve passes through the intervertebral foramen. This is the spinal ganglion, and it is limited to the dorsal root. In the horse each of the various rootlets possesses its ganglion (Fig. 139). There is no ganglion on the ventral root. Dorsal and ventral roots unite outside the intervertebral foramen to form the ordinary mixed spinal nerve. The functions of these two roots is quite opposite. In the dorsal roots the impulses are passing from the periphery to the centre; they are afferent fibres, and from the fact that they convey impulses which give rise to sensations of various kinds, they are also known as 'sensory.' In the ventral roots the impulses are passing from the centre to the periphery; they are efferent nerves, and, from the fact that the majority of the efferent impulses result in movement, they are also known as 'motor' nerves. A portion of cord embracing a pair of spinal roots is spoken of as a segment, and the spinal cord consists of a series of such segments united end to end.

Passing away from the spinal cord in company with the ventral roots is a branch known as the *white ramus communicans*. So soon as it gets outside the vertebræ it leaves the ventral root and passes to a portion of the nervous system known as the 'sympathetic.' The sympathetic system is frequently regarded as a something quite distinct from the ordinary cerebro-spinal system, and in function this is very largely the case; but the white ramus communicans serves to remind us that the two systems are very closely linked, and under one central authority. It is unnecessary here to follow the white ramus any farther; it will be fully considered with the sympathetic system.

Function of the Spinal Nerves.—If the dorsal spinal roots be divided, all parts supplied by them below the division lose sensation; if the portion of nerve in connection with the spinal cord be irritated, pain is produced. The spinal sensory fibres endow the whole body with sensation, with the exception of certain parts of the face. If the ventral roots be divided, all parts supplied by the nerves below the seat of division suffer motor paralysis; if the cut end of the nerve still in connection with the tissues be irritated, the muscles contract vigorously; while if the piece of nerve in connection with the cord be irritated, nothing happens. In this way it is demonstrated that the sensory impulses pass into, whilst the motor impulses pass out of, the cord. Sometimes pain is felt when the motor roots are divided, due to one or two branches of the sensory nerves finding their way back into the cord by this channel. The phenomenon is known as *recurrent sensibility*.

Columns of the Cord.—If a cord be suitably prepared, a transverse section (Fig. 137) shows it to consist of two similar halves, united by a comparatively small central mass of tissue, through the centre of which a minute longitudinal canal runs. The halves are separated by fissures on the dorsal and ventral surfaces of the cord. The ventral median fissure is wide, and does not reach down to the centre, while the dorsal median fissure is narrow and deep. Each half of the cord is seen to consist of dorsal, lateral, and ventral columns, separated from each other by a shallow longitudinal groove. A section of the cord shows it to be made up of both white and grey matter, the latter, internally placed, forming the medulla. This is arranged something like the letter **H**, or like two inverted commas placed back to back. The shape of the grey matter on transverse section depends entirely on the region of the cord examined. This may be seen in Fig. 136, which shows three sections of the cord. The dorsal and ventral ends of the comma, or crescent-shaped halves of the grey matter, are spoken of as the cornua. From the dorsal cornu the afferent or sensory fibres run; from the ventral run the efferent or motor roots. The white substance of the cord also varies in thickness (see Fig. 136). Stated generally, the cord increases in white matter from the tail to the head. The grey matter is largest in the cervical and lumbo-sacral enlargements, and this increase and decrease in size corresponds with the in-

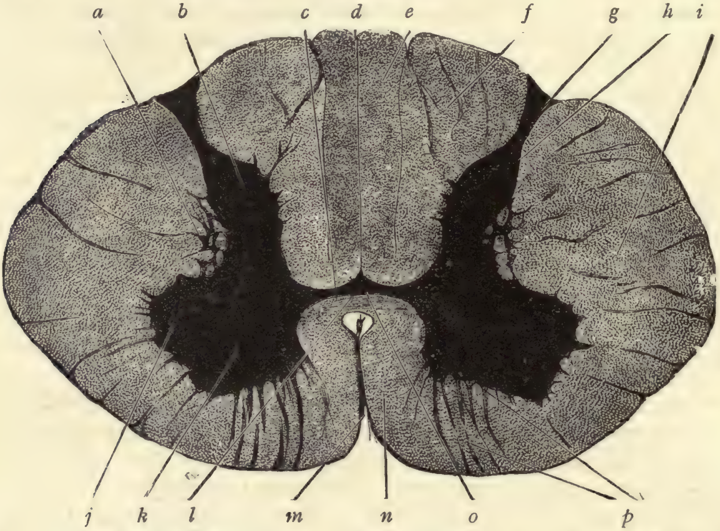

FIG. 137.—TRANSVERSE SECTION OF THE SPINAL CORD IN THE CERVICAL REGION × 8D. THE LINES IN THE LATERAL AND SUPERIOR COLUMNS RUNNING FROM THE OUTER MARGIN ARE LAMINÆ OF THE PIA MATER (M'KENDRICK).

a, Processus reticularis; *b*, dorsal horn; *c*, grey commissure; *d*, dorsal septum; *e*, Goll's column; *f*, superior column; *g*, point of entry of dorsal root; *h*, substantia gelatinosa; *i*, lateral column; *j*, large multipolar nerve-cells; *k*, ventral horn; *l*, white commissure; *m*, inferior longitudinal fissure; *n*, inferior column; *o*, central canal; *p*, point of exit of ventral roots.

crease and decrease in the number of nerves entering and leaving the cord in these regions.

The **Grey Matter of the Cord** may be regarded as a pair of long columns extending throughout its length. These columns, when examined microscopically, are found to consist mainly of nerve-cells, some of which are connected with the dorsal, others with the ventral roots of the spinal nerves. A collection of nerve-cells possessing afferent and efferent nerves is essentially a ganglion, and, regarded in this light, the grey matter of the spinal cord may be considered to be built up of a series of ganglia placed end to end and communicating. In the ventral cornu of the grey matter the cells are largest and arranged in groups. The cells, as we have already seen (p. 435), are multipolar ; their axon is the origin of the fibre of the ventral or motor spinal root. All the motor nerves obtain their nerve-cell origin in the inferior cornu, and wherever the outflow of nerves is the greatest, as in those parts of the cord opposite to the limbs, there these cells are largest and most definitely grouped. There is another group of cells in the ventral cornu which is not connected with the building up of motor nerves ; their axons pass from the grey into the white matter, and travel up, down, and across the cord, where they constitute short tracts of white matter, which knit together the various segments. These are known as 'association fibres.' Between the ventral and dorsal cornua is a portion of grey matter known as the 'intermedio-lateral column.' In this part are the cells connected with the nerves which link up with the sympathetic system, and supply the viscera by means of the *white rami communicantes*. The cells in the dorsal horn of the cord are smaller, and the cell-groups not as well marked. There is, however, a group of large cells extending throughout the dorsal grey matter, known as 'Clarke's column.' It furnishes fibres which pass into the white substance of the cord, and form there what is known as the *direct cerebellar tract*.

The **White Matter of the Cord** consists of medullated nerve fibres, generally running longitudinally ; structurally, these fibres differ from those found in the body-nerves by the fact that they possess no neurilemma, the medullary sheath being contained within a supporting material known as *neuroglia*. The white matter of the cord is divided into certain columns—dorsal, lateral, and ventral. These anatomical columns give no notion of the physiological paths which exist between the brain, cord, and body. These paths in the white matter have been mainly worked out by the degeneration method—viz., by studying the degeneration which follows division of the spinal nerves. If, for example, cutting the dorsal roots above the spinal ganglion leads to the degeneration of tracts in front of the injury, it is known this must be a sensory or ingoing path; if the degeneration occurs behind the injury, it is evident that the affected fibres have their cell-station farther forward, and that the path is motor or outgoing. Another method of tracing the tracts is the developmental. In the early embryo the fibres have no myelin sheath; when, later on, this appears, it is observed that all the fibres belonging to the same group are simultaneously invested with myelin. In this way it is possible to determine the fibres possessing a common course. There are other methods of inquiry which need not here be referred to; sufficient has been said to indicate the nature and difficulties of this class of investigation.

Paths in the Cord.—The white matter forms paths in the cord which are spoken of as ascending and descending tracts.*

The ascending and descending tracts in the spinal cord of man have only been mapped out after years of laborious research, in which pathological as well as physiological results have been utilised. In man the tracts are numerous and complex; as the animal scale is descended simplification occurs. The monkey is less complex than man, but more complex than the dog, and so on. Tracts present in man are absent in the lower animals; for instance, a tract known as the *direct pyramidal*, which connects some motor centres in the brain with the limbs and muscles concerned, has no representative outside of man and the higher apes. Another, known as the *crossed pyramidal tract*, and well represented in man and the monkey, is but insignificant in the dog (see Fig. 138). The columns of white matter in the spinal cord of the domesticated animals have not been clearly made out, with an exception to be mentioned presently, and we shall, in consequence, be compelled to refer to the columns in man in order to illustrate the principle on which the work is carried out. The white tracts do not run unbroken throughout the length of the cord; some are long and others short; some disappear for good; others change their relative positions at different levels. Speaking generally, the descending tracts diminish in size from the head towards the tail; the ascending tracts diminish from the tail to the head. The shorter tracts are probably the older ones developmentally, for long tracts are more conspicuous in highly-developed animals in which the independent activity of the cord is imperfectly retained, while short tracts are associated with more independent function of the spinal cord and less development of the higher centres.

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* These terms have been retained for quadrupeds in preference to the expressions 'headwards' and 'tailwards,' or 'forwards' and 'backwards.'

Descending Tracts in the Cord.—These run from the brain to the spinal cord in the ventral columns of the white matter, and give off aborisations to the motor neurones of the ventral or motor roots of the spinal nerves (Fig. 139). Most probably there are other descending paths not yet discovered, but those which are clearly known are as follows :

Direct Pyramidal Tract.
Crossed Pyramidal Tract.
Rubro-spinal Tract.
Proprio-spinal Descending Tracts.

Direct Pyramidal Tract.—This is only found in man and the anthropoid apes. It is associated with complex, skilled, and delicate muscular movements, such as occur in man, and it is through this channel that these movements are produced and directed. The more highly developed the brain, the larger the direct pyramidal tract. In Fig. 138 the position and relative size of this tract in man is shown. Both pyramidal tracts are spoken of as *cortico-spinal*, to indicate that they connect the cortex of the cerebrum with the spinal cord.

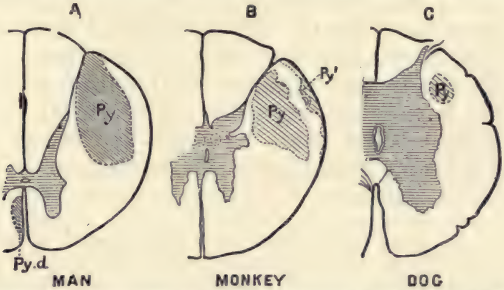

FIG. 138.—DIAGRAM TO ILLUSTRATE THE RELATIVE SIZE OF THE CROSSED PYRAMIDAL TRACT (Py) IN THE DOG, MONKEY, MAN (FOSTER, AFTER SHERRINGTON).

In B, Py′ is an outlying portion of the pyramidal tract separated from the rest by the cerebellar tract. Py.d in A is the direct pyramidal tract only present in man.

Crossed Pyramidal Tract.—This is the main descending motor path in animals (Figs. 138, C; 139, A). Nevertheless, it is relatively smaller than in man, for the size of this tract bears some relation to the size of the motor areas in the brain. Where these are small, as in the horse, ox, and sheep, the tract is small. Small motor areas suffice for animals such as the horse, where the limb movements are of a simple pendulum type. The combined areas of the two pyramidal tracts in man constitute nearly 12 per cent. of the total cross area of the cord. The following shows the proportion the crossed pyramidal system bears in other animals :

Cat	7·76
Rabbit	5·30
Guinea-pig	3·00
Mouse	1·00
Frog	Absent

The crossed pyramidal tract is so named on account of its fibres crossing in the medulla on their way to the cord. In the direct pyramidal tract there is no crossing. The effect of the fibres crossing is that the right cerebrum controls the muscles on the left side of the body, and *vice versa*. If an animal be shot in the right brain it falls on the left side, as these muscles are the first to be paralysed.

In the dog, and perhaps in other of the lower animals, there are other paths than the pyramidal conveying impulses which lead to motion, for if all the pyramidal fibres be divided, complete paralysis does not follow, while stimulation of the motor areas of the cerebrum continues to produce muscular contraction. It is believed that the supplemental path is the *rubro-spinal tract*, which takes its origin in the red nucleus of the mid-brain, and is considered by Dexler* to replace in animals the direct pyramidal tract.

Recently J. L. King has investigated the crossed pyramidal tract of the sheep.† He finds it to be imperfectly developed, and that it does not extend beyond the first cervical segment. In the medulla some of its fibres decussate, others are uncrossed. This short tract represents all the motor fibres having origin in the cortex of the cerebrum; from this we should expect that not only are the cortical motor areas small, but that motor fibres must be derived from some other portion of the brain. King has found this to be the case. In the ventro-lateral columns of the cord of the sheep are two well-developed descending paths running its entire length. One of these he identifies as the rubro-spinal tract. These two tracts represent in the sheep the chief primary motor paths in the cord. Centrally they are connected with the mid-brain, pons, and medulla. The fibres are consequently sub-cortical in origin. The two motor paths are reinforced by proprio-spinal fibres, which brings them into intimate relation with near and distant segments of the cord. King concludes that the chief motor paths in the spinal cord of lower mammals do not, as in man, originate in the central cortex, but from a point lower in the brain.

Rubro-Spinal Tract.—Known also as the *Ventro-Lateral Descending Tract*, lies just below the crossed pyramidal tract (Fig. 139, A).] It arises in the mid-brain from the red nucleus.

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* 'Veterinary Anatomy,' S. Sisson.

† The *Quarterly Journal of Experimental Physiology*, vol. iv., No. 2, June, 1911.

King considers that one of the two well-marked motor paths in the sheep represents the rubro-spinal tract of some other animals. This tract in the dog is referred to above.

The *Proprio-spinal descending tract* or tracts consists of fibres which connect the more anterior spinal segments with the more posterior. The fibres of these in the dog are much more numerous than the pyramidal tract fibres, and their importance lies in the fact that they connect the four limbs together in locomotion.

Ascending Tracts.—These are as follows :

- The *Direct or Dorsal Cerebellar Tract* (tract of Flechsig).
- The *Median Superior Tract* (column of Goll).
- The *Lateral Superior Tract* (column of Burdach).
- The *Ventro-lateral Ascending or Ventral Cerebellar Tract* (tract of Gowers).

The *Direct or Dorsal Cerebellar Tract* (Fig. 139, A) arises in the peculiar group of cells in the grey matter on the inner side of the dorsal horn. The axons from these cells run to the cerebellum without crossing. This tract forms a long afferent path, and it has been made out that the fibres from the lumbar portion of the cord lie outermost ; the dorsal fibres lie within these ; and, finally, the fibres from the anterior dorsal and lowest cervical nerve are most inwardly placed. The whole of the fibres comprising this tract do not reach the brain ; many terminate in the cord. The tract terminates in the cerebellum, which it enters by the posterior peduncle.

The *Median Superior Tract* lies on either side of the dorsal median fissure. The fibres composing it are small, and the path terminates at the bulb. Degeneration of the tract occurs when the dorsal roots of the cord are divided. This tract is made up of long fibres of the dorsal roots of the tail, pelvis, and hind-limbs, and runs up and ends mainly in the bulbar nucleus of Goll, often called the *leg* nucleus. In Fig. 139, A, this tract corresponds to the sensory path marked ' hind-leg ' and ' tail.'

The *Lateral Superior Tract* is derived from long fibres of the dorsal roots of the thoracic region, fore-limbs, and neck. It runs up and ends mainly in the bulbar nucleus of Burdach (*nucleus cuneatus*) commonly spoken of in man and the monkey as the *arm* nucleus. In Fig. 139, A, this sensory path is indicated by the portion marked ' fore-leg,' ' neck,' and ' trunk.'

The Ventro-Lateral Ascending, or Ventral Cerebellar Tract.—The precise seat of origin of this tract in the cord is unknown. Division of the dorsal roots of the spinal nerves produces no effect upon it. Its origin must therefore be within the cord. The tract terminates in the cerebellum, entering by the anterior

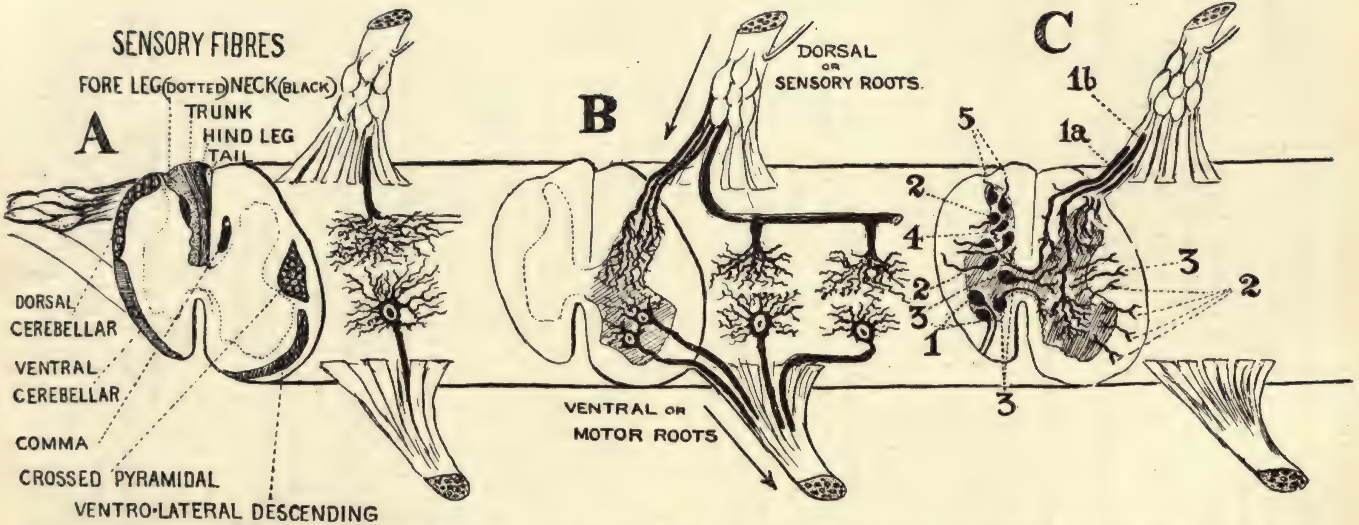
SENSORY FIBRES
FORE LEG (DOTTED) NECK (BLACK)
TRUNK
HIND LEG
TAIL
A
DORSAL CEREBELLAR
VENTRAL CEREBELLAR
COMMA
CROSSED PYRAMIDAL
VENTRO-LATERAL DESCENDING
B
DORSAL OR SENSORY ROOTS.
VENTRAL OR MOTOR ROOTS
C
1b
1a
5
2
4
3
2
3
1
3
2

FIG. 139.—DIAGRAM OF THE SPINAL CORD SHOWING THE STRUCTURAL FEATURES BY WHICH SOME OF ITS PRINCIPAL FUNCTIONS ARE CARRIED OUT.

A is a sectional view of the cord, which may be conveniently referred to the cervical region, the head being to the left of the observer. B and C are to be visualised as sectional transparencies.

A

The right segment of the cord, the farthest from the observer, shows the *ascending tracts*; the left segment shows the *descending tracts*.

In the dorsal portion of the right half of the cord is shown the relative position of the sensory root fibres connected with the limbs, trunk, and tail, contained in the columns of Goll and Burdach, that of Goll being nearest to the central line.

In the lateral and ventral columns of the same side are shown the other ascending paths, the *dorsal cerebellar* from Clarke's column of the same side, the *ventral cerebellar* chiefly from the grey matter of the opposite side.

In the left half of the cord are shown the descending or motor tracts. The *comma* tract, not referred to in the text, consists probably only of root fibres in the dorsal column; the *crossed pyramidal* tract as indicated, and below this the *ventro-lateral descending* or *rubro-spinal* tract. The dorsal and ventral roots are seen united on the far side, with ganglia on the dorsal roots.

B

The spinal roots are shown as separated. The method by which they enter and leave the cord is indicated, the arrows pointing in the direction taken by the impulses. The mechanism concerned in a simple reflex act is shown diagrammatically, the incoming fibre arborising around cells in the grey matter, the impulse travelling out by the ventral root, or passing up the cord, arborising later, and so passing out. A more complex system consists of another neurone placed between those already shown.

C

In the right segment of the cord are shown the nerve cells, in the left the entering nerve fibres.

Right side: (1) *Motor cells* giving origin to the ventral roots; (2) *tract cells*, the axons passing into the white matter of lateral and ventral columns; (3) *commissural cells*, the axons of which cross the cord; (4) *Golgi cells, second type*, the axons of which do not leave the grey matter; (5) *tract cells*, the axons passing into the white matter of dorsal columns.

Left side: 1, *a* and *b*, entering fibres of sensory roots; 1*a*, ending in Clarke's column of same side, and dorsal column of opposite side. 1*b*, sensory fibres arborising around cells of ventral roots of same side. Below 1*b* are fibres to the lateral and superior column of same side. 2 and 3 are collateral fibres, 2 for the ventral and lateral columns, 3 from the pyramidal tract, arborising around motor cells in the ventral portion of the grey matter.

peduncle. The fibres terminate by arborising around cells in the middle lobe of the organ.

Association Fibres.—Certain short fibres, previously mentioned, arise in the cord, and form tracts uniting the various segments. They originate from 'tract cells' in the grey matter of the cornua, and from here run into the white substance, and after a short course they run back and re-enter the grey matter. These tracts may be ascending or descending; their function is to knit together the various spinal segments.

The above ascending and descending tracts do not account for the total amount of white matter; there are still unmapped regions in the cord.

When the various ascending tracts reach the medulla, they undergo change in form, position, and distribution. Some, as we have seen, terminate in cells in the bulb—in fact, there are only two upward paths which pass through unbroken—viz., the two cerebellar. In the descending tracts, which are passing from the cerebrum and cerebellum to the cord, only one—the pyramidal tract—passes through unbroken. All the others behave as those of the ascending tracts—viz., terminate in a collection of cells—spoken of as 'nuclei'—and from these fresh fibres arise.

Functions of the Ascending Tracts.—In the *median superior* and *lateral superior tracts* and the dorsal columns of the cord impulses are conveyed which lead to a sensation of pressure (touch), but more especially impressions from skeletal muscles, tendons, and joints, known as *muscle-sense*, to which is due the co-ordination of muscles in locomotion. It will be remembered that the lateral superior tract is almost wholly composed of sensory fibres from the muscles. These impulses are carried up the same side of the cord on which they entered. In the bulb the paths end, fresh fibres are formed, and cross to the opposite side, to terminate in the cerebrum, in the area known as that of the *body-senses*. Injury to the fibres of body-sense produces an awkwardness in gait; the animals show a want of skill in using the hind-limbs. The muscles are there, but, owing to the loss of muscle-sense, they do not know it, and consequently are unable to direct their movements.

The *dorsal cerebellar tract* and the *ventral cerebellar tract* carry impulses connected with deep sensibility, arising from muscles, tendons, and joints. Each of these tracts terminates in the cerebellum; it is believed they are also associated with muscular co-ordination, which, as we shall see later, is the special function of the cerebellum.

The *lateral superior tract* is the path for the transmission of impulses giving rise to sensations of pain, heat, and cold;

perhaps, also, some touch impulses are conveyed, but little is known regarding this. The pain and temperature fibres end in the grey matter after entering the cord, and from these fresh axons are formed, which run up both sides of the cord. In the medulla the fibres terminate, and fresh axons arise from its cells, which pass to the optic thalamus of the opposite side. This is the chief station for all varieties of afferent stimuli. In both the ascending and descending paths there are fibres terminating in the cord — *i.e.*, not running the full length of the tract. This is especially the case with the afferent fibres, the larger number of which enter the grey matter, where many terminate by arborising around tract cells. Many tract cells furnish further fibres, which continue onwards to maintain the path.

All sensory impulses pass to the brain on the side opposite to their origin, and all motor impulses leave the brain on the opposite side to that to which they are distributed, so that injury to a left motor area leads to a right body paralysis (see Fig. 141).

The termination of the sensory fibres in the cord has been in part referred to. Having passed through their cell-station in the ganglion on the dorsal spinal nerve, they enter the cord, but do not directly pass along it as an afferent tract, but penetrate the grey matter, where many terminate (Fig. 139, A); others are provided with a fresh axon, and then continue the headwards passage as a spinal tract. As a matter of fact, the entry of the fibres into the cord is by no means so simple as the above would suggest, and it is further complicated by the fact that the fibres on entering the cord divide into a **Y** or **T**, one passing backwards for a short distance, the other forwards, both, perhaps, giving off collaterals (see Fig. 140). Some of these collaterals establish cell-communication with the grey matter, and so to the motor system, a reflex arc being thus formed (Fig. 139, A and B). The reflex arc may be complicated by the introduction of an inter-

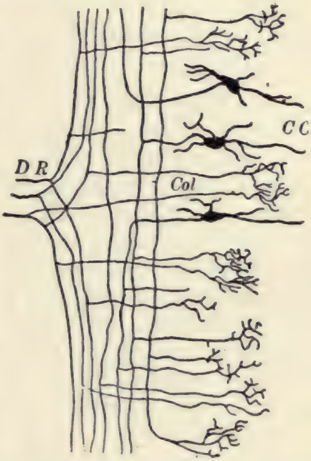

FIG. 140.—BRANCHING OF DORSAL ROOT FIBRES IN CORD (DONALDSON, AFTER RAMON Y CAJAL).

DR, dorsal root fibres entering the cord, and dividing **Y**- or **T**-wise into fibres running forwards and backwards, which give off collaterals, *Col*. Cells, CC, can be seen in the grey matter of the cord with which the collaterals establish communication.

mediate set of neurones, connecting the cell-termination of the sensory nerve with the cell origin of the motor.

Special Centres in the Spinal Cord.—In the cord certain centres exist, which, though ordinarily under the control of a chief centre in the bulb, yet are capable, as we have seen, of carrying on peculiar reflex actions even after the cord has been divided.

The *cilio-spinal centre* lies between the cervical and dorsal portions of the cord ; in it fibres originate which through the cervical sympathetic supply the dilator muscle of the iris. Destruction of the region in question causes a contraction of the pupil, whilst irritation of it causes the pupil to dilate. The *ano-spinal* centre, found in the lumbar portion of the cord, controls the act of defæcation ; it would appear to be highly developed in herbivora, which possess the power of bringing it into play not only when the body is at rest, but during movement. The functions of the ano-spinal centre appear rather complex, inasmuch as it has not only to maintain the tone of the sphincter, but also to relax it during defæcation, and under the latter condition simultaneously to contract the abdominal muscles and diaphragm. These, however, are brought about quite simply through the reciprocal innervation of antagonistic muscles (see p. 456). The *vesico-spinal* centre also exists in the lumbar portion of the cord, and governs micturition ; its action is similar to that of the ano-spinal centre. In the lumbar portion of the cord other centres are found—for example, the *erection* centre, the *genito-spinal* centre which contains the nervous apparatus employed in the emission of semen, and the *parturition* centre. *Vasomotor* centres are found throughout the cord ; they are principally under the control of similar centres in the bulb, but may act independently. All these centres in the cord are activated through the sympathetic system.

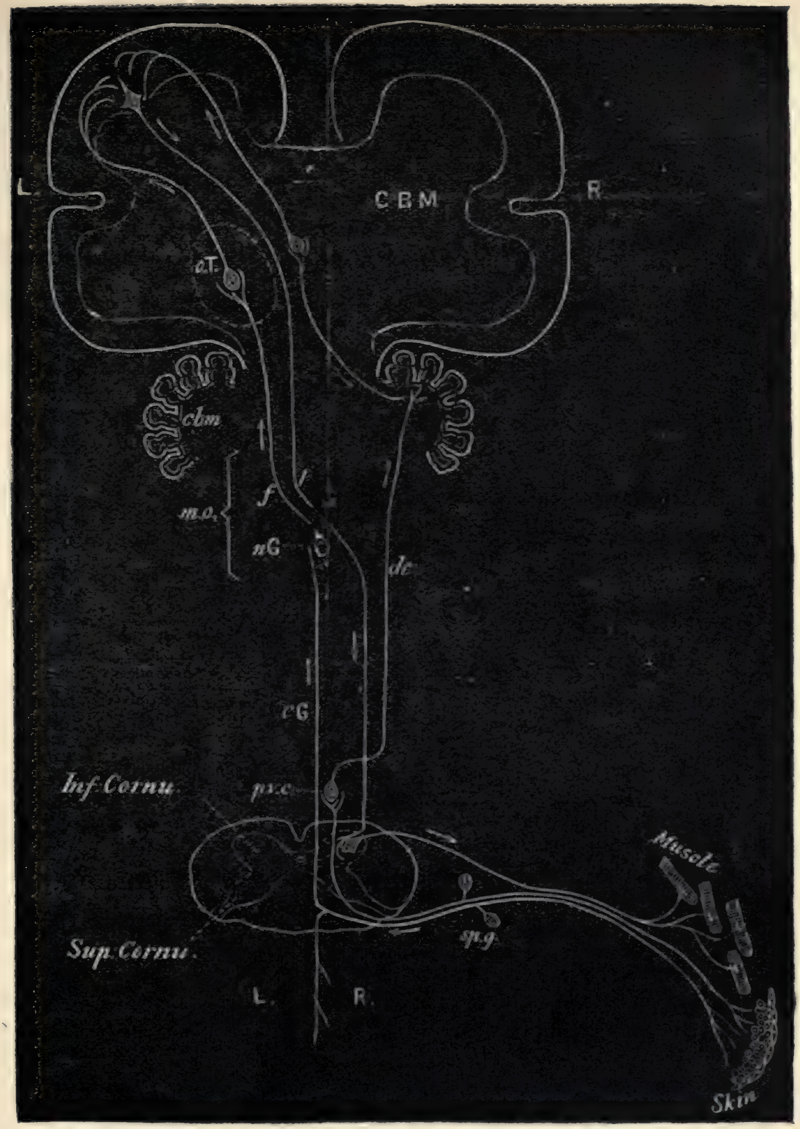

FIG. 141.—DIAGRAM OF THE AFFERENT AND EFFERENT PATHS PASSING TO AND FROM THE BRAIN BY THE CORD (SHERRINGTON).

L, Left ; R, right ; CBM, cerebrum ; *cbm*, cerebellum ; *mo*, medulla oblongata, containing the decussation of *p*, the pyramidal tract, and of *f*, the fillet ; the decussation of *f* should really be a little higher instead of a little lower than that of *p* ; *n*G, nucleus gracilis (Goll's) ; *o*T, optic thalamus ; *pvc*, the superior vesicular column, or column of Clarke ; *sp g*, spinal ganglion ; *c*G, median superior column (Goll's) : *dc*, direct cerebellar tract.

The arrows show the direction of the impulses. An afferent impulse, say from the skin, passes along the sensory nerve, through the spinal ganglion, and enters the dorsal columns of the cord ; it may pass to the cerebrum direct viâ the medulla by *c*G, the median superior column, which crosses in the bulb, and so gains the opposite side of the brain ; or the impulse may pass by *dc*, the cerebellar tract, to the cerebellum, entering it on the same side, and from here crossing over to the opposite cerebral hemisphere. An efferent impulse originates in the cerebral cortex, gains the pyramidal tract, passes through the bulb to the *opposite* side of the cord, enters the cells in the inferior cornu of the grey matter, and passes out in the inferior spinal nerves. The arrows denote the direction of the impulses.

SECTION 4.

Bulb (Medulla Oblongata), Pons, and Mid-Brain.

The change undergone by the spinal cord merging itself into the bulb may be studied by successive sections of the latter. Briefly it may be stated that the central canal of the cord widens in order to become subsequently the fourth ventricle ; the symmetrical and regular arrangement of the grey and white matter of the cord becomes broken up, not only in order that it may find its way to its destination in the higher centres, but in the case of those fibres which are passing out, that they may be collected from the various outlying centres, and brought together in an orderly manner in the smaller and more compact structure, the medulla. But the medulla is not only a highway for nerve-fibres passing in two opposite directions — it is also a cell-centre; and besides restarting all the tracts which terminate in the bulb on their way up or down, it also gives origin to six of the most important cranial nerves. The origin of these in the medulla, in the various grey nuclei, is an additional complication to the rapidly changing appearance presented by the organ in successive sections from rear to front. Apart from the complexity of the subject we are now entering on, which increases as we approach the cerebrum, there is also the important fact that in the large herbivora, with but few exceptions, the course of the fibres and the collocation of cells, not only in the bulb, but also in the other centres, are not known with any degree of accuracy.

There is now good reason to hope that the experiments of King* and other observers on the larger herbivora, will be the means of laying the foundation of exact physiological knowledge with regard to their nervous system.

The bulb in the horse is wider and more flattened than the cord ; it is about 2 inches in length, and is wider anteriorly than posteriorly ; it is considered to begin at the first cervical nerve and end at the pons. In this short length of nervous material functions of vital importance are carried out, through the medium of those cranial nerves which take their origin from this part. On the ventral surface of the medulla two well-marked structures exist, known as the *pyramids*. There is no surface enlargement indicating the presence of the *olivary bodies*, so prominent a feature in man, but in the substance of the medulla well-marked olivary nuclei exist. The pyramids are formed by the collection of motor fibres descending from the brain, and brought together in two bundles in the bulb. In the pyramids they decussate, so that fibres from the right brain pass down the left side of the cord, and *vice versa.* It is more convenient to build up the bulb from below, so that, though the pyramidal fibres are passing out of the brain, they are, from a constructional point of view, spoken of as if they were passing the other way. This being so, it is usual to describe the pyramidal fibres in the cord as crossing in the medulla, and by so doing cutting through the ventral horns of the grey matter, and eventually causing them to disappear, as may be seen from sections taken at a higher level. In this way the pyramids are formed, and little is left of the original grey matter. On the dorsal surface of the bulb the two horns open out ; the tip of each swells, and forms the *substantia gelatinosa*, while the *columns of Goll* and *Burdach*, which, it will be remembered, have their fibres passing into the brain, end in nuclei known as the *nucleus gracilis* and *nucleus cuneatus* respectively. These are often called the 'leg' nucleus and 'arm' nucleus. The fibres from the above columns terminate by arborising around the cells in these nuclei ; those from the anterior half of the body terminate in the *nucleus cuneatus*, while those from the posterior half terminate in the *nucleus gracilis.* From the cells in these nuclei fresh axons are formed, which pass forward into the higher centres, and so still further increase the complicated arrangement of the bulb. Incidentally attention may be drawn to the fact that this is the second cell-station on the sensory path, the first being the ganglia on the dorsal roots of the spinal nerves. The fibres passing forward into the higher centres mentioned above form the *internal arcuate fibres*, and in their journey forwards decussate above the pyramids, and continue their course through the bulb and pons under the name of the *fillet*, and so reach the optic thalamus ; here, for the third time, the fibres arborise around cells. The *fillet*, or *lemniscus*, is consequently the sensory path connecting the between-brain and the body.

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* *Op. cit.*

These changes in the arrangement of the medulla having brought the central canal of the cord close to the dorsal surface, it soon opens out into the fourth ventricle ; and now a further complexity in the arrangement of the bulb is evident from the fact that the nuclei giving origin to the cranial nerves enter the field, those of the tenth and twelfth pairs being seen forming the grey matter of the floor of the fourth ventricle. A fresh mass of grey matter also appears, known as the *olivary body*, while further *internal arcuate fibres* cross to the opposite side, enter the *restiform* body which forms the posterior peduncle of the cerebellum, and so gain access to the cerebellum. Some of these arcuate fibres enter the restiform body on its own side. The *restiform body* is formed from the direct cerebellar tract of the cord. The fibres of this tract terminate in the median hemisphere, or *vermis*, of the cerebellum by arborising around the Purkinje cells of the body. Other fibres connect the medulla with the cerebellum, for fibres pass from the *olivary body* through the restiform body of the opposite side to the cerebellum.

Such, briefly, is the arrangement of the bulb. It is better for the purpose of description to continue carrying the sections forward both through the pons and mid-brain.

The **Pons** lies between the bulb and the cerebral peduncles. If a section be made through it, the appearance presented does not differ materially from that furnished by a section of the upper extremity of the medulla, with the exception that bundles of fibres taking a transverse course are passing to the middle peduncles of the cerebellum. Between these fibres is the grey matter, or *nuclei pontis*. From the dorsal surface of the pons is formed the *anterior cerebellar peduncles*. Fibres course through the pons from one side of the cerebellum to the other, and from the cerebrum to the pons. The pyramidal fibres reach into the pons, and are spoken of as the *cortico-pontine*. Though the fibres are described as reaching into the pons from the pyramid, it will be remembered the flow is in the opposite direction, and that these fibres are passing from the cerebral cortex backwards into the cord. In this section can be seen the *nucleus of Deiters*, a collection of large multipolar cells, in the floor of the fourth ventricle, which is intimately connected with afferent and efferent mechanisms, and is one of the cell-terminations of the vestibular branch of the eighth nerve. From the pons arise the important fifth pair of cranial nerves.

A section through the **Mid-Brain** shows that the reticular structure of the pons is continued forward ; it is enlarged by fibres derived from the opposite cerebellar cortex, and fibres from the nuclei of the fifth and eighth cranial nerves. The nervous mass formed by these structures bifurcates into the *crura cerebri*, or *cerebral peduncles*, and these constitute the ventral portion of the mid-brain. Each peduncle is divided by a groove into two portions—a dorsal, known as the *tegmentum*, and a ventral, or *crusta*. Between the two is a collection of grey matter known as the *substantia nigra*. In the crusta the motor, and in the tegmentum the sensory fibres are contained ; it therefore constitutes an important highway between the cerebrum and the body.

Functions of the Bulb.—We have seen that this is the path by which the brain communicates with the periphery and the periphery with the brain. It gives origin to, or is connected with, all the cranial nerves but those of smell, vision, and the muscles of the eyeball. It is the supreme reflex centre for all the important functions of life, such as respiration (p. 133), circulation (p. 84), the action of the heart (pp. 52, 57), and the digestive apparatus from the mouth to the large intestine. It is astonishing that these varied functions can be controlled by a few inches of nervous tissue. If the medulla be cut off from the brain in front of its various centres, the animal continues to live, respirations are regulated, the blood-pressure is maintained, and the heart continues under control. If the section be made behind the centres, all is at once changed, because the respirations cease instantaneously; the blood-pressure sinks dangerously, but then partially recovers, rising in the cat and dog to a height of about 90 mm. (instead of the normal 130). The heart beats slowly but well, and the animal dies from asphyxia (see p. 134). If artificial respiration be established, the beat of the heart may be maintained for a day or more. The animal is conscious, feels pain if the lip be pinched, blinks when the finger approaches the eye, feels hunger, and will even seize food within its reach, masticate and swallow it (Chauveau).

The centres located in the bulb are those for mastication, swallowing, sucking, vomiting, respiration, phonation, coughing, the regulation of the heart-beat and arterial calibre, movements of the iris, the secretion of saliva, the glycosuria centre, a centre for the sweat glands, and a centre for shivering. It is not proposed to deal here with these centres; they have received sufficient notice in the various chapters in which the above questions have been considered.

The **Mid-Brain** is composed of the *corpora quadrigemina* and *cerebral peduncles ;* these form the basal ganglia.

The Corpora Quadrigemina.—The white matter of the anterior of these bodies is derived from the optic nerve, the fibres of which arborise around its cells. Fibres from the corpora quadrigemina also run backwards to the cord, and in man gain a tract known as the infero-lateral descending. The anterior pair of bodies is concerned in vision. It forms a reflex arc connected with the movements of the pupil, while, through its connection with the optic nerve, it works upon the muscles of the eyeball. The posterior corpora quadrigemina are important in the higher group of vertebrates—viz., birds and mammals which have a cochlea—that is, a 'hearing' ear—besides an 'equilibrating' ear. They receive fibres from the cochlear nerve, and have reflex centres concerned with the lower auditory functions and with vocalisation.

The Optic Thalamus, as we have previously seen (p. 471), is the junction for all afferent impressions prior to distribution to their destination ; it is the main sensory relay station to the cortex. It is considered to be the seat of painful impressions, for lesions of it are associated with acute pain on the opposite side of the body. Its structure suggests that it is also connected with motor functions, for destruction of portions of the cortical area leads to degeneration of their corresponding nuclei in the optic thalamus. Connected with the thalamus is the *red nucleus*, which gives origin to an important spinal motor path in the lower animals (see p. 466). It is supposed that the thalamus is associated with reflex mimetic movements of gesture, physiognomical expression, and of primitive vocalisation. In lesions of the thalamus emotional expressional movements of the human face are lost. Some observers have considered that secretory, vasomotor, and other fibres connected with the sympathetic system, are represented in the thalamus.

The Corpus Striatum.—Lesions of this body are said to be associated with a rise in temperature ; hence it has been looked upon as governing heat production. Little is known of the subject, but it is supposed that impulses pass to the skeletal muscles, causing an increased production of heat. Developmentally the corpus striatum is a part of the cerebral cortex, and not a portion of the old mid-brain. The corpus striatum is interesting clinically on account of the comparative frequency with which it is diseased in the horse. There are no symptoms pointing to cerebral trouble until a day or two before death. It is remarkable the size to which a growth in this body may attain before any symptoms of pressure are shown. These cases should enable the question to be settled of the connection, if any, between the corpus striatum and body temperature. Experimental injury of the corpus striatum of the horse was carried out by Colin, who found that a simple puncture caused no inconvenience or interference with locomotion. Three fresh punctures made in the same corpus produced immediate paralysis of the hind-legs, and the animal could only be kept standing with a support under the belly. When walked thus supported, the fore-limbs were quite unaffected, the hind-limbs dragged. If the animal fell, power appeared to be regained in the hind-legs, for he was able to recover the standing position. The paralysis gradually passed away, and the horse was able to stand without assistance.

SECTION 5.

The Cerebellum.

The cerebellum is broadly divided into a central body, known as the *vermis*, or worm, on either side of which are the *hemispheres*. It is situated above and in front of the medulla, and is remarkable for the curious foldings of its grey and white matter, which give it a characteristic appearance on section. The grey matter is placed externally, a reversal of the order found in the cord. The grey matter of the cerebellum is found to consist microscopically of two layers, an outer and inner. In the *outer or molecular layer* two types of cells are found: one is known as a 'basket cell,' from the peculiar manner in which its axon dips down and encloses the large characteristic cells of Purkinje, which are placed between the outer and inner layer of the cortex (Fig. 142). In the second type of cell found in the outer layer of the cortex the axons run longitudinally to the surface of the cerebellum, giving off collaterals which dip down and arborise around the dendrites of the cells of Purkinje. In the *inner or granular layer* of the cortex the cells are small, their axons travel towards the surface of the cerebellum, where a **T**-piece is formed, which, running parallel to the surface, makes connections with the dendrites of the Purkinje and other cells, such as those of Golgi's second type, which are also present. Purkinje's cells, as above mentioned, are placed between the two layers of the cortex. They are distinguished by their considerable size and by possessing a single dendrite, which breaks up into a remarkable branching tuft and runs towards the surface of the organ, while the axon passes into the white matter, giving off collaterals (Figs. 143 and 144).

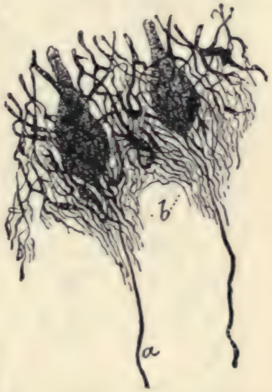

FIG. 142. — PERICELLULAR BASKETS (SCHÄFER, AFTER RAMON Y CAJAL).

Two cells of Purkinje from the cerebellum are seen surrounded by end ramifications forming a basket-work: *b*, derived from the branching of axons; *a*, of small nerve-cells in the molecular layer.

The white substance of the cerebellum consists of both afferent and efferent fibres; the afferent fibres—viz., fibres afferent for the cerebellum—are found microscopically to consist of two varieties, which, from peculiarities in their arrangement and distribution, are known as '*moss*' and '*tendril*' fibres. The 'moss' fibres terminate by branching in the nuclear layer of the grey matter, while the 'tendril' fibres pass into the molecular layer, and arborise by climbing around the dendrites of the cells of Purkinje. The efferent fibres are the axons of the cells of Purkinje, which are essentially efferent in function. The above outline affords some notion of the complexity of the structure of the cerebellum; it is anticipating matters to say that this body is an important reflex arc, but it is evident from its structure how well it is arranged for reflex processes.

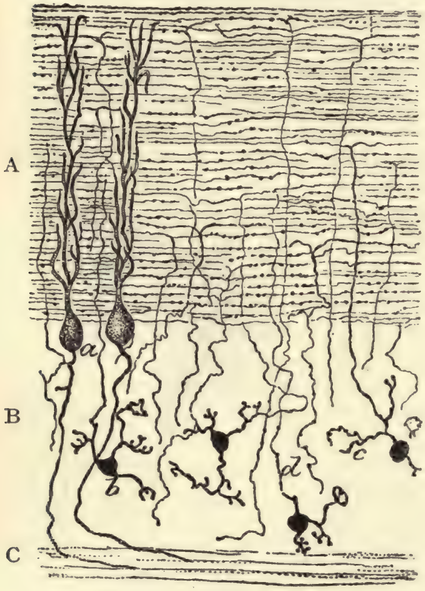

Fig. 143.—Cerebellar Cortex: Section in Direction of Lamina (Cajal).

A, Outer or molecular layer; B, inner, nuclear, or granular layer; C, white matter. *a*, Purkinje's cell; *b*, granule cells of inner layer; *c*, dendrite of a granule cell; *d*, axon of a granule cell passing into the molecular layer, where it bifurcates into two fine longitudinal branches (Golgi's method).

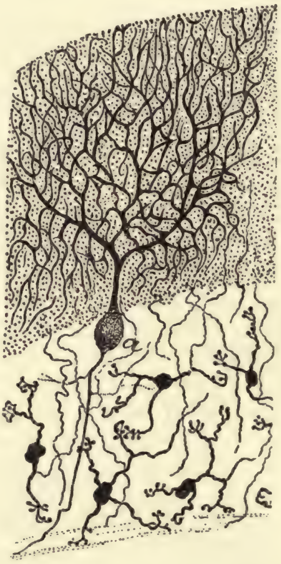

Fig. 144.—Cerebellar Cortex: Section across a Lamina (Cajal).

a, Purkinje's cell; the numerous dots in the molecular layer represent cross-sections of the bifurcated axons of the granule cells (Golgi's method).

The cerebellum, by means of its three peduncles, is brought into connection directly or indirectly with all the other parts of the brain. The incoming fibres sweep through the peduncles and terminate in the grey matter in the manner already described. The efferent fibres originating in the cells of Purkinje do not pass out through the peduncles directly as fibres derived from the cortex ; these cortical fibres first terminate in nuclei, and from the cells of the nuclei fresh fibres are formed.

Through the *anterior peduncle* fibres pass from the cells of Purkinje to the mid-brain. This is the only purely efferent tract assigned to the cerebellum, and the distribution of the fibres is peculiar and complex. The peduncles converge and meet in the mid-brain ; by so doing their fibres decussate, so that impulses from the cerebellum pass to the opposite side of the brain, where they are conveyed to the red nucleus. This is the second cell station for the efferent fibres. In the red nucleus, part of the fibres are sent upwards to the cerebral cortex by means of fibres known as *thalamo-cortical,* and part pass backwards by a special tract known as the *bundle of Monakow,* or *rubro-spinal tract,* which in its passage to the medulla crosses the central line, so that impulses pass down the lateral columns of the cord on the same side as they issue from the cerebellum. In this way, broken as it is, the cerebellum is brought into communication with its own side of the cord, which is in contrast with the connection existing between the cerebrum and spinal cord, which is crossed. By means of the anterior peduncle the fibres of the *ventro-lateral ascending tract* of the cord (tract of Gowers) also gain entrance to the cerebellum, being distributed to the lower part of the *vermis.*

By means of the *middle peduncle* the cerebellum is brought into communication with the *pons,* while from nuclei in the pons fibres pass to the cerebrum. This is the second indirect path between the cerebrum and cerebellum, but in this case it is afferent—viz., the communication is from cerebrum to cerebellum.

Through the *posterior peduncle,* which is formed by the restiform body of the medulla, another important afferent path is opened up to the cerebellum, but in this case from the spinal cord. The direct cerebellar tract passes unbroken through the bulb, through the posterior peduncle, its fibres being mainly distributed to the *vermis* on the same side. Other very important fibres are conveyed by this peduncle from the eighth pair of cranial nerves, constituting a connection between the cerebellum and the labyrinth. The eighth pair of nerves arises from two roots ; one from the vestibule of the ear is in no way connected with the sense of hearing, but is entirely devoted to the question of body equilibrium and allied matters. This branch gains access to the cerebellum through the posterior peduncle. It will be observed that the posterior peduncle is a second afferent path to the cerebellum.

The cerebellum is connected, as we have already seen, with the mid-brain, cerebrum, medulla, and spinal cord. It is doubtful whether its two halves are connected. Afferent impulses may pass to the cerebrum via the cerebellum, and efferent impulses from the cerebrum to the muscles may reach them through the cerebellum. Afferent impulses may pass to the cerebellum and efferent impulses issue from it without the intervention of the cerebrum.

Functions of the Cerebellum.—Our knowledge respecting the uses of this organ is still very incomplete. Little more is known of its functions than was first demonstrated by Flourens in his classical experiments carried out over eighty years ago. He regarded it as being connected with locomotion and the problem of body-balance. The study of comparative anatomy lent support to this theory ; it was observed how highly the cerebellum was developed in birds and in swift swimming fishes with great locomotive power, such as the shark. In birds the *vermis* of the cerebellum is large and deeply folded, though its hemispheres are almost wholly absent, excepting in those birds which remain some time in the air and possess wings and feet of considerable strength. The experiment of Flourens on the cerebellum consisted in its removal in the pigeon ; as the result of the operation the animal was unable to fly, stand, or feed itself. When it attempted to walk, spasm of the extensor muscles of the legs occurred, and it fell, struggling wildly, in a state of evident panic. There was no muscular paralysis, but the pose of the body was awkward, the head being drawn back and twisted. During the muscular spasms the contractions led to the animal turning somersaults. In course of time the violent symptoms disappeared, and the animal was able to fly, but for a long time was unable to perch, through spasms of the extensor muscles of the limbs. When the cerebellum is sliced away, and not entirely removed, the gait is rendered uncertain and staggering, and there is an inability to maintain equilibrium.

In the dog injury to one hemisphere of the cerebellum leads to the animal moving in a circle or rolling towards the injured side, and to a disturbance of co-ordination. The entire cerebellum, however, has been removed in the dog, and the animal remained alive for many months. In these cases there are muscular spasms of the head, neck, and fore-legs, weakness of the hind-limbs, and when the eyes are closed standing is impossible. When the acute symptoms pass away the animal is left with a deficiency of muscular tone. It is interesting to note that this lesion does not prevent the dog from swimming.

Colin exposed the cerebellum in a draught horse, and punctured the middle lobe, or *vermis*, with a scalpel. The animal at once shook his head, but there were no convulsions. After a second and third puncture the gait became staggering and the limbs splayed to preserve the equilibrium. When the animal walked, the body was balanced alternately to the right and left, as if at each step he expected to fall. He then showed a marked tendency to lean forward in the attitude of draught, as if determined to negotiate a stiff hill ; it was only with difficulty that seven or eight assistants held him back.

The cerebellum has been regarded as the centre of muscle sense—*i.e.*, as the centre by which the position of the body and its movements are recognised in the absence of visual and tactual impressions. The necessary impulses are brought to it from the footpads in soft-footed animals, also from the depths of the body—*i.e.*, the muscles, tendons, ligaments, joints (pp. 458, 470) —and, as we shall presently see, from the internal ear. Loss of sensation in the soles of the feet in man leads to disturbances of equilibrium ; in animals this does not appear to be present. A cat may have its feet desensitised by division of all sensory nerves with no evident interference with locomotion, and in the solid-footed horse robbing the part of sensation gives similar results.

The question of maintaining the body equilibrium, a function markedly lost as the result of injury or disease of the cerebellum, (cerebellar ataxia), is explained by the connection which exists between the cerebellum and the internal ear. This connection is the most important path by which afferent impressions associated with the mechanism of equilibration are conveyed. The nerve from the semicircular canals enters the pons and connects with the nucleus of Deiters, which in turn connects with the cerebellum. Some fibres may even pass direct to the cerebellum. Through the nucleus of Deiters the vestibular nerve is brought into indirect communication with a nucleus which gives rise to the nerves supplying the muscles of the eyeball, and by means of the vestibulo-spinal tract it establishes connection with the motor cells in the spinal cord. The influence of the semicircular canals on equilibration will receive consideration with the organs of special sense, but it is due to afferent impressions received by the cerebellum from the semicircular canals that the cerebellum is enabled to judge of the position of the body in space. Other afferent impressions arising in the muscles and joints convey to the cerebellum impulses which maintain the muscles in a condition of reflex tonus, enable the attitude of the body to be maintained during rest, and co-ordinated movement to be executed during locomotion. It will be remembered that this explanation of the action of the cerebellum is due to the researches of Sherrington.

The receptors of the labyrinth, and those of the deep receptors of joints and muscles, he shows are stimulated by the animal itself, while the surface receptors (*extero-ceptors*) are stimulated from without. The deep receptors (*proprio-ceptors* of a limb can, however, only influence the tonicity of the muscles of that limb, while those of the labyrinth not only influence the limbs and the trunk, but the head and muscles of the eyeball. In consequence the limb influences are mainly concerned with the relation of the limbs to other portions of the trunk, while the influences from the labyrinth regulate the position of the body generally towards the external world and gravitation. Sherrington regards the chief ganglia of these important functions as being located in the cerebellum.

The maintenance of equilibrium and sense of direction are associated with movements of the eye muscles, the labyrinth furnishing the necessary information of the relationship of the body to surrounding objects. One of the earliest indications of disease of the spinal cord may be an inability to walk in the dark, and we have seen that a dog without a cerebellum cannot move with the eyes covered. The cerebellum is furnished with the needful information through its connection with the third and fourth pairs of cranial nerves, which govern the movements of the eyeball. It would appear that the biped derives more information from perceiving the position of the limbs relatively to the body than is afforded the quadruped, whose eyes are in advance of the limbs. The writer has never known a horse refuse to advance, even on the darkest night, provided the ground be good. If broken, he travels with care ; if boggy, he may refuse to advance. Without seeing his limbs or surrounding objects, he moves as safely in the dark as in the light, while his sense of direction over ground he has previously travelled is so excellent that the man who has lost his way may safely leave the solution of the problem to his horse.

Each half of the cerebellum controls the muscular system on its own side of the body, and each half receives impulses from the opposite cerebrum. It appears likely that definite regions of the cerebellum govern definite body areas. It can be shown experimentally that a particular region of the cerebellar cortex controls movements of the fore-foot, another governs a hind-foot ; others cause rolling or bending movements of the body, or conjugate movements of the eyes. The posterior portion of the *vermis* is concerned mainly in muscular co-ordination, and in some of the lower animals is the only portion of the cerebellum represented. Finally, we have seen that, after experimental removal of the cerebellum, muscular co-ordination may still be established, which suggests that this organ cannot alone be the seat of this function.

SECTION 6.

The Cerebrum.

The cerebrum is composed of grey and white matter, the grey being externally placed like a mantle and thrown into convolutions. The use of the convolutions is to increase the surface of the grey matter, and their depth has been supposed to bear some relationship to the intelligence of the animal. There are many animals whose cerebra are quite smooth; there are others, like the bear, seal, and whale, whose cerebra are much more convoluted than in man.

Weight of brain in relation to body weight has been suggested as a measure of intelligence, and when the comparison is made among animals of the same group it may be possible that the heavier brains are the more intelligent. Weight of brain may, however, depend upon such factors as fluid, white matter, and grey substance. Colin compiled an elaborate series of tables of weight of the cerebral nervous system in animals, and showed that the proportion of brain to body weight was as follows:

Man	1 to 52
Cat	1 ,, 99
Dog	1 ,, 235
Rabbit	1 ,, 295
Sheep	1 ,, 317
Ass	1 ,, 332
Pig	1 ,, 369
Horse	1 ,, 593
Ox	1 ,, 682

For every kilogramme of body weight—

Man requires	19·00	grammes of brain.
Cat requires	11·37	,, ,,
Dog requires	4·80	,, ,,
Rabbit requires	3·31	,, ,,
Sheep requires	3·00	,, ,,
Ass requires	2·46	,, ,,
Pig requires	1·90	,, ,,
Horse requires	1·68	,, ,,
Ox requires	1·47	,, ,,

In proportion to its size a mouse has more brain than a man, thirteen times more than a horse, and eleven times more than an elephant; a cat has much more than a dog; a rabbit nearly approaches a dog. It is evident that outside its own group the relative weight of brain to body is of limited value. The modern method of determining the mind of an animal from the structure of the cortex of the cerebrum will be dealt with later on.

Structure of the Cortex.—The cerebral cortex is regarded as made up of several layers of cells, the number of which is not agreed upon by histologists, but may be regarded as consisting of four principal layers. These layers vary in different animals, and we are compelled, as in other portions of the physiology of the nervous system, to fall back upon what is known of the matter in the dog, pig, and man, in the absence of direct information regarding the horse. The layer of cells immediately beneath the pia mater is spoken of as the *molecular;* it consists of some very small nerve-cells with their dendrites and axons, also of dendrites projecting from cells deeper seated in other layers, and the terminal processes of axons which end there belonging to fibres coming from other regions. Perhaps the distinct feature of the layer is the structure first spoken of, the small cells with their dendrites and axons. These begin and end in this layer, and appear to be of a linking-up, or, as it will be described later, associative nature. In the second layer are *small pyramidal cells,* with the apex towards the surface and the axon passing inwards to the white substance. The depth of this layer increases the higher the animal scale is ascended. Next comes a layer of *large pyramidal cells,* sometimes called 'giant pyramids of Betz,' found mainly in that portion of the brain anterior to the fissure of Rolando,* and in particular in the region of that fissure. These cells are of great physiological importance, as from them the fibres constituting the great motor tracts are derived. The last layer is that of *polymorphous cells,* which are, generally speaking, small, and many of them fusiform in shape. With these are cells of Golgi of the second type; but whereas the axons of the former pass inwards to form white fibres in the medullary portion, the axons of the Golgi cells pass outwards and end by arborising in the molecular layer. The function of the cerebral cortex has been examined, not only by the method of direct experimental excitation, but also from its histological side; this has enabled the cortex to be mapped out into different regions, and in this connection it is desirable to make it clear that the histological method does not wholly consist in comparing the structure of one fully-developed area with another, but in studying the period when the fibres leading to the area assume their sheath of myelin, both in the embryo and young animal. This line of research is especially associated with the name of Flechsig. The study of the structural features of the brains of imbeciles and other pathological conditions, have also largely contributed to a more exact knowledge of the use of the various parts of the cortex.

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* It is convenient for the present to retain the term 'fissure of Rolando'; it will be pointed out later that there is no fissure of Rolando in the dog, nor is the *crucial fissure* of this animal, in the vicinity of which the motor area is located, the equivalent of the fissure of Rolando.

The structure of the cortex points to it being a reflex arc, the complexity of which differs according to the animal scale. The cortex of man and the frog possesses the same anatomical elements, but the complexity of the neurones of the former ~~are~~ is in marked contrast to the simplicity which distinguishes those of the frog (see Fig. 145). A rich system of dendrites means more numerous and complex connections. Apart from this evidence has recently been brought forward to show that there are structural peculiarities accompanying specialisation in function, to which attention will be drawn later.

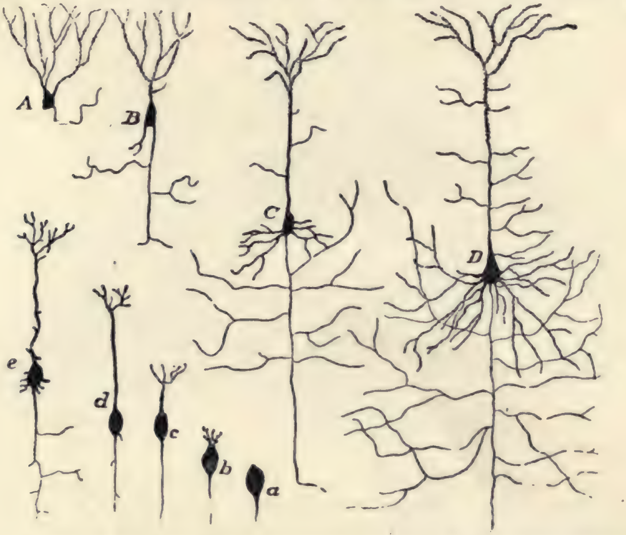

FIG. 145.—PYRAMIDAL CELLS OF CEREBRAL CORTEX IN DIFFERENT ANIMALS (DONALDSON, AFTER RAMON Y CAJAL).

A—D shows the different degree of complexity in the fully-developed pyramidal cells in different vertebrates : A, frog ; B, lizard ; C, rat ; D, man. *a*—*e* Shows the development of the pyramidal nerve-cells of the cerebral cortex in a typical mammal : *a*, neuroblast with commencing axon ; *b*, dendrites appearing ; *d*, commencing collaterals.

In the white substance of the cerebrum are nerve fibres conveying impulses to the cortex, either from its different parts or from the basal ganglia, bulb, and cord. There are also efferent fibres which have their origin in the cells of the cortex, which pass to different parts of the brain, and out of the brain via the bulb and cord. Fibres which pass from one part of the cortical convolutions to another belong to the linking or *association* system (Fig. 146). Fibres which pass to the opposite side of the brain via the corpus callosum belong to the *commissural* system, while the masses sweeping out from the cortex and connecting it with the mid-brain, pons, bulb, and spinal cord, belong to the *projection* system. In Fig. 147 the projection system in the human brain is shown. It is not wholly efferent—that is to say, it does not consist entirely of motor fibres passing out to the pons, bulb, and spinal cord. The motor tracts only form a part of the projection system, which in addition contains sensory, visual, and auditory tracts, and fibres travelling from the frontal lobes to the cerebellum.

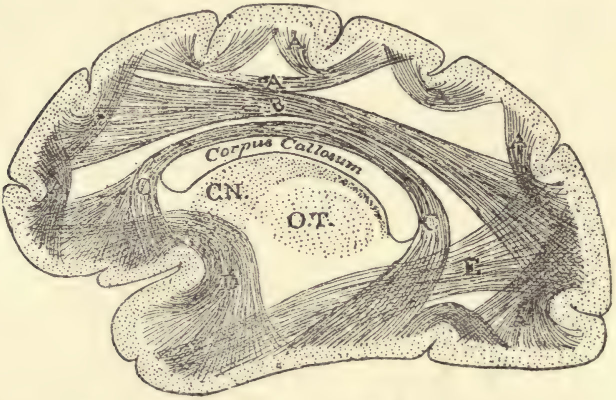

FIG. 146.—ASSOCIATION FIBRES (AFTER STARR).

Human cerebral hemisphere seen from the side. A, A, association fibres between adjacent convolutions; B, between frontal and occipital lobes; C, cingulum, connecting frontal and temporo-sphenoidal lobes; D, uncinate fasciculus between frontal and temporal regions; E, inferior longitudinal bundle between occipital and temporo-sphenoidal lobes; O.T., optic thalamus; C.N., caudate nucleus.

The Great Efferent or Motor Path in man is formed, as we have just seen, from the large pyramidal cells in the cortical layer of that portion of the cerebrum anterior to and bordering on the fissure of Rolando, and travels backwards and downwards through the corona radiata, internal capsule, and peduncles of the cerebrum to the pons (Fig. 147, B). In this region are detached the motor fibres connected with the cranial nerves, and these cross to the opposite side of the brain. The larger mass sweeps onwards through the bulb, and in the pyramids the system decussates, the fibres crossing to the opposite side of the cord. In the cord cell-connections are formed all the way along, either by means of collaterals or by the fibres actually terminating; in either case synapses are formed around the cells in the ventral horns of grey matter. From these axons arise which eventually form the motor root of the spinal nerves. The motor roots pass to the muscles, where they terminate in an *end plate*. It will be observed that there are two neurone systems in this path, one between the cortex and the cord (pons for the facial muscles), the other between the cord and the muscle. From the moment these fibres start on their journey from the cortex, connections are formed with neighbouring structures by means of synapses, not only in the cortex, but mid-brain, pons, bulb, and, as we have seen above, in the cord. It has even been considered that in their passage along the cord the two tracts exchange fibres from opposite sides. In this way is formed the

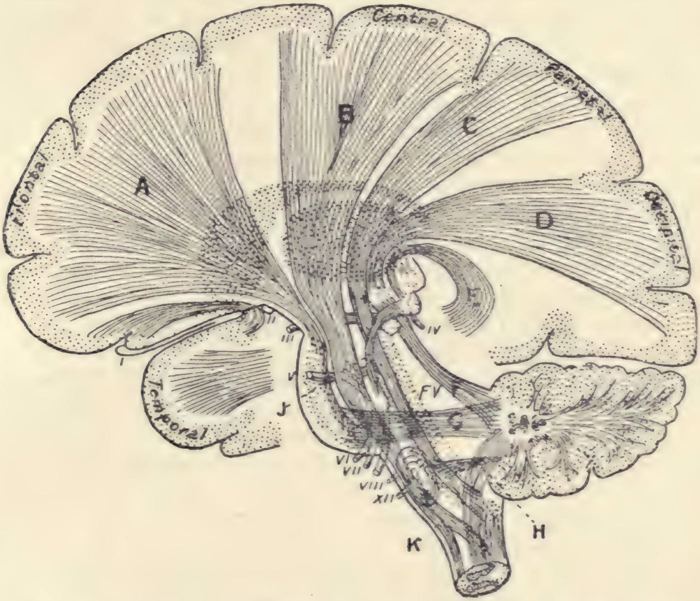

FIG. 147.—PATHS FROM CORTEX IN CORONA RADIATA, HUMAN (STARR).

A, tract from frontal convolutions to nuclei of pons and so to cerebellum; B, motor pyramidal tract; C, afferent tract for tactile sensations (represented in the diagram as separated from B by an interval for the sake of clearness); D, visual tract; E, auditory tract; F, G, H, superior, middle, and inferior cerebellar peduncles; J, fibres from the auditory nucleus to the posterior corpus quadrigeminum; K, decussation of the pyramids in the bulb; FV, fourth ventricle. The Roman numerals indicate the cranial nerves.

tract for voluntary body movement which we have studied at p. 465 under the name of the 'crossed pyramidal tract.' It is the path by which movements of which the animal is distinctly conscious are effected. The brain starts or instructs the movement, the mechanisms in the cord carry it out. This places quadrupeds in much the same position as the decerebrated frog. The apparently purposeful movements executed by the cord of the animal immediately after death warrants this supposition. The limbs are represented in the cortical area of the fissure of Rolando, and they are also represented in the grey matter of the spinal cord, the great difference between the two centres being that one can be exercised voluntarily, while the other is involuntary and unconscious, until the moment arrives when the pulling of the needful switch brings it under the control of the higher centres.

We shall see presently that the entire cerebral cortex may be removed from the frog, pigeon, and dog, and the motor area from the sheep, without producing in these mammals more than a marked loss of power, which is regained in time. In such cases the centres in the cerebrum controlling the muscles are entirely cut off from them, and other tracts have to be found. In the dog it is suggested that the rubro-spinal tract (p. 466) fulfils this function. In the sheep we have seen (p. 466) that motor fibres are only in part derived from the cerebral cortex, and that a sub-cortical supply is furnished by the mid-brain, pons, and medulla. There can be little doubt that a similar arrangement exists in the other herbivora.

The double neurone relay between cortex and end plate is the explanation of a peculiarity observed in muscular paralysis in man. When the neurone between the cord and the muscle is affected, the paralysis is complete; but when the pyramidal neurones—viz., those between the cortex and the grey matter of the cord—are affected, there is a path left open for reflex stimulation, and those impulses normally passing to muscles from the cerebellum, which have been spoken of as 'tonic,' throw the paralysed limbs into a condition of continuous contraction. This is spoken of as *spastic paralysis*.

The Great Afferent or Sensory Path conveys impulses evoking sensations—heat, cold, touch, and pain—also such senses as are not normally recognised—viz., muscle sense, joint, tendon, and viscera sense, and the senses of vision, hearing, smell, and taste. This path is broken by at least three sets of synapses: (1) in the cord; (2) in optic thalamus; and (3) in cortex cerebri. The optic thalamus is practically the meeting-place or junction of the whole afferent system on its way to the cerebral cortex (Fig. 141).

Impulses conveyed by sensory nerves pass through the spinal ganglion, enter the spinal cord, and reach the medulla by the dorsal columns of the cord. In the dorsal columns of the cord they travel on the side they enter, and finally reach the medulla in the gracilis and cuneate nuclei, where they arborise. Through the fresh fibres there formed the impulses cross to the other side of the medulla, and by means of the *fillet* reach the mid-brain and optic thalamus. From the thalamus the fibres are distributed by means of the internal capsule to that portion of the cerebral cortex not occupied by the motor areas in front and behind the fissure of Rolando. Impulses which, though afferent, are probably not sensory, but for reflex work, gain the medulla via Clarke's column. The spinal roots on entering the cord arborise around the cells in this column, and by means of the fibres forming the dorsal and ventral cerebellar tract they reach the brain as follows. The dorsal (direct) cerebellar tract passes by means of the restiform body into the superior part of the *vermis*, while the ventral cerebellar tract runs along the lateral columns to the pons, passes beneath the roots of the fifth nerve, and then bends back to end in the superior vermis of the cerebellum. It is by means of the lateral columns that pain-provoking impressions are conveyed from both halves of the body. These impulses having reached the pons, they pass to the optic thalamus, which is the sensory relay station to the cortex and the seat of pain.

The **Association System** of fibres is employed in bringing the various parts of the brain into connection—convolution with convolution, lobe with lobe, cerebrum with mid-brain, cerebellum, and pons. Some fibres, the **commissural,** connect the right side with the left in all its anatomical parts, the *corpus callosum* being the largest member of this system. The system of association fibres links up the various parts of the brain and affords routes innumerable for the passage of impulses to and fro. It has been previously mentioned that the complexity of the dendrites of the cells bears some relation to the scale of brain development in the animal kingdom ; it may now be noted that the more profusely branched the dendrites the larger the number of paths there are in the association system.

Functions of the Cerebrum.

The cerebrum is without sensation ; it can be handled, cut, or otherwise injured without any sign of pain being elicited. For many years it was considered, in consequence of the experiments of Flourens, that the cerebrum was a homogeneous organ, and all of its parts functionally of the same character. It was known to be connected with the higher faculty of intelligence, but that it was an organ containing within itself other organs functionally distinct, yet intimately connected, was never anticipated.

We have seen that the decerebrated frog is a reflex machine, but with animals so low in the scale it is difficult to obtain any real knowledge of the function of the organ.

Removal of the Cerebrum.—The pigeon with the cerebrum removed becomes converted into a drowsy, lethargic animal, unable to feed itself, though it may try in an aimless manner to do so. It can fly and perch, may be wakened by a loud noise, shows no fear, and is not possessed of a maternal feeling. It may awake sufficiently to preen itself, gape, and then once more returns to its condition of somnolence. So far as can be judged, the chief loss this animal has experienced is that of memory.

Colin removed the cerebra in horses. He notes that the animal fell almost before the superficial layer had been taken away. The horse so dealt with was unaffected by stimulation, gave no indication of feeling pain, noises were not heard, light had no effect upon the pupil, and there was no eyelid reflex. Ammonia applied to the nostrils caused no irritation, and taste and all special senses were lost. In the decerebrated heifer the animal was able to stand, but could not see ; hay was held in the mouth and not masticated,* and no notice was taken of the blowing of a horn.

If partial destruction of one hemisphere in the horse be practised, the animal may be kept on its legs for a short time. The superficial layer of the right cerebral lobe was removed in the ass, and the animal remained standing for nearly an hour. The limbs on that side were slightly bent under the influence of the body weight, and the animal moved with difficulty, and, if left to himself, remained immobile. When made to walk he walked very quickly, now and then in a circle in the direction opposite to the lesion. If he walked into anything, he fell, but could be raised. In another ass the left hemisphere was incised in the direction of its length, and immediately hemiplegia occurred on the right side ; the animal fell on that side, and could not be got up again. In many horses a puncture through the entire thickness of the cerebral lobes sometimes sufficed to cause the animal to fall and to be unable to rise. Bovines withstood far better than equines mutilation of the cerebral lobes. A heifer with one cerebral lobe removed remained standing for more than half an hour, retained its vivacity, and walked with such ease that it was extremely difficult to observe the muscular deficiency on the opposite side to the lesion. When the remaining lobe was removed, she could still stand up, but could only move forwards, backwards, and turn with great difficulty.

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* A common symptom in the horse suffering from brain trouble.

Injury to one cerebral peduncle in the rabbit was found by Longet to lead to ménage movements towards the opposite side ; but if the peduncle were cut through, the movements did not occur. Colin found that ménage movements were performed by the horse when a cerebral peduncle was injured. He pricked the left peduncle, and observed that the head was at once carried to the right, and the neck and body bent, so that the muzzle became applied to the flank, and sometimes to the thigh, as if the animal were bent in halves; the limbs were gathered in a bunch under the body, and the animal rotated on a small pivot. When turning, it frequently fell, but the body still remained curved ; when raised, the circular movements were repeated. The horse could go backwards, but could neither advance nor turn to the left.

Colin destroyed the corpus callosum, and observed that he produced neither pain nor convulsions. Longet cut into it throughout its length in young horses and young rabbits, and found there was no sign of pain. The animals remained standing, but could walk or run about if made to. Colin repeated the above experiment on two horses. Both remained standing for a short time ; one then fell backwards after some movement of the muscles of the eyeball ; the other showed great muscular weakness, and fell on his side. There were no convulsions in either case.

All these observations by Colin were made before anything was known of the function of the cerebrum in connection with skeletal muscles. The crossed nature of the pyramidal tract in these animals was clearly proved, and the great independence of the spinal cord in bovines demonstrated.

Goltz removed both cerebral hemispheres, step by step, in a dog, and succeeded in keeping the animal alive for eighteen months. It became a most interesting psychical study. The animal was a mere reflex machine. It could see, but not comprehend ; it would show signs of hunger, eat when the nose was brought in contact with the food, but could not recognise food placed near it. After the paralysis succeeding the operation had passed away, the dog could walk slowly and stupidly with its head down. It would growl or bark, turned its head to the spot if stimulated, but did not bite. The face was expressionless, and the tail was never wagged. It rejected food of a disagreeable nature, such as meat soaked in a solution of quinine. No matter how hungry, this was refused, though the gustatory centres had been removed. The animal slept, but did not dream. She exhibited no sexual excitement or œstrum. Memory, emotions, and the capacity to learn were absent ; anger was a prominent feature. Goltz's dog exhibited it every day for eighteen months each time she was fed.

A point in the history of this dog has now been reached which is of extraordinary veterinary interest. The animal in its roaming on one occasion wounded its hind-foot ; *it was then* *observed to walk lame, holding the injured foot off the ground.* It is possible to urge that pain was felt, as some portions of the brain-stem had been left intact; but Sherrington's remarkable experiment on the decapitated cat disposes of this.* A cat so treated cannot stand, but it can perform stepping movements with its limbs. 'If, as the preparation lies on its side, one hind-foot be forcibly pinched, this limb is flexed . . . and the other limbs at once begin rapid, co-ordinated stepping movements. The injured foot is held up out of harm's way, and the other legs run away.'†

Removal of an anterior lobe of the cerebrum in the dog leads to unilateral motor and sensory paralysis; the motor paralysis is recovered from, but the loss of muscle sense remains. Removal of the posterior lobes of the cerebrum leads to blindness; there is no paralysis, sensory or motor; the dog remains obedient, but sluggish. Sherrington cut the brain off from the heart and viscera in the dog by division of the cord in the lower cervical region. The animal showed joy, anger, fear, and sorrow. Nothing would induce it to eat dog's flesh, but in this case the olfactory and gustatory paths were still open; in Goltz's dog they had been removed. That 'dog will not eat dog' is a very old maxim, but travellers in the Arctic have recorded the fact that they will do so as occurring under stress. Nevertheless, it is remarkable that both the idiot created by Goltz, and the dog furnished by Sherrington, with no knowledge of its stomach, should refuse to eat their own kind. In this matter they furnish a far nicer discrimination than man.

Observations on man, begun in the Franco-German War and continued on animals, have demonstrated that the cortex, which it must now be made clear is the elaborating part of the cerebrum—as distinct from the white or connecting matter—contains an area which controls the voluntary muscles of the body, and is known as the **motor area.** There is another area connected with body sensibility, such as *muscle sense, touch, pressure,* and *temperature.* This is known as the **sensory area,** and comprises not only the body senses above mentioned, but the special senses of *sight, hearing, taste,* and *smell.* The position of these is known in the sheep, dog, monkey, and man with considerable accuracy, so that maps of the hemispheres have been drawn up indicating the function of its localities; the subject is generally spoken of as the *localisation of cerebral function.*

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* *Brain,* part cxxix., vol. xxxiii., 1910.

† These astonishing results show that lameness may be purely reflex in origin. The question of the fitness or unfitness of chronically lame cases to perform work will in time have to be considered afresh. The above observations show with what justice the veterinary profession, as the result of pure observation, has urged in a court of law, though generally without success, that an animal suffering from lameness is not necessarily suffering pain.

The Motor Area.—A region of the brain of the monkey or man, known as the *fissure of Rolando,* is intimately connected with the cells which give rise to the motor nerves passing to muscles. In the dog there is no *fissure of Rolando,* but there is a fissure, known as the *frontal* or *crucial sulcus* (Fig. 148, *c.s.*), in which the motor cells for the muscles are localised as in the fissure of Rolando, and similar localities must exist in other animals, although, with the exception of the sheep, dog, cat, rabbit, and monkey, little has been done to identify them.

If the brain in the region of the crucial sulcus of the dog be exposed, and the part stimulated electrically, the muscle, or group of muscles, contract which are connected with those cells of the cortex immediately beneath the electrode. It is remarkable that a great European war was necessary to demonstrate this fact, but physiologists for years remained in this matter under the influence of the teachings of Flourens and Majendie, who stated that the cerebral cortex was inexcitable. Gradually the knowledge derived from stimulation of the cortex has accumulated, until a very remarkable picture of the cortical functions can be obtained. Fig. 149 shows the motor area of the chimpanzee; that for man is still more complex. The size of a motor area bears a relation to the degree of complexity of limb movements. The limb movements in quadrupeds are simple; for instance, in the horse they are mainly pendular; in the dog they are more complicated; and still more so in the cat, in which the delicate movements of face-washing are necessarily of a

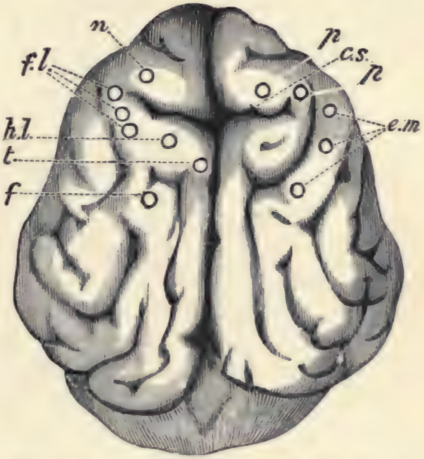

Fig. 148.—Motor Areas of Dog's Brain (Stewart).

n, Neck; *f.l.*, fore-limb; *h.l.*, hind-limb; *t*, tail; *f*, face (the position here assigned to the facial muscles is unusual, it is generally more laterally situated, and farther forward); *c.s.*, crucial sulcus; *e.m.*, eye movements; *p*, dilatation of the pupil in both eyes, but especially in the opposite eye.

The areas are only marked on the left side of the figure except the eye areas, whose position, to avoid confusion, is indicated on the right hemisphere.

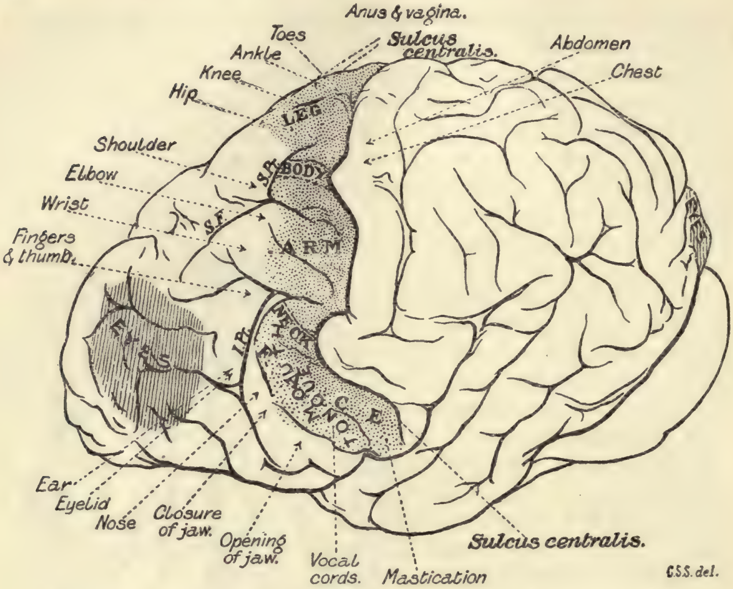
Anus & vagina.
Toes
Sulcus centralis.
Ankle
Knee
Hip
Abdomen
Chest
Shoulder
Elbow
Wrist
Fingers & thumb
LEG
BODY
S.P.
S.F.
ARM
EYES
I.F.
NECK
FACE
TONGUE
Ear
Eyelid
Nose
Closure of jaw.
Opening of jaw.
Vocal cords.
Mastication
Sulcus centralis.
C.S.S. del.

FIG. 149.—MOTOR AREA OF CORTEX OF CHIMPANZEE (GRÜNBAUM AND SHERRINGTON).

Lateral aspect of the hemisphere.

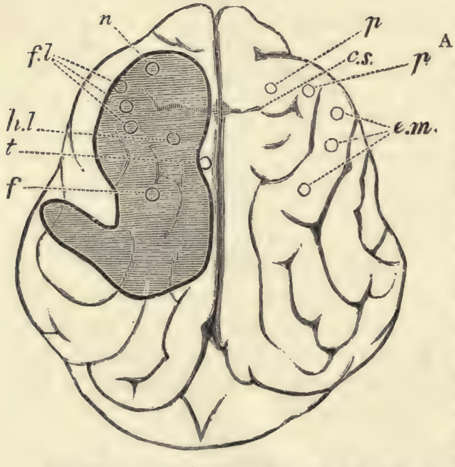
n
p
c.s.
p'
f.l.
h.l.
t
f
e.m.

FIG. 150.—DOG'S BRAIN WITH LESION (STEWART).

A portion of the cortex indicated by the shaded area was destroyed by cauterisation. The symptoms were complete blindness of the opposite eye (in this case the right); weakness of the muscles of the limbs and of the neck on the right side; slight weakness of the limbs on the left side. When the animal walked, there was a tendency to turn to the left in a circle. In eating or drinking, the head was turned to the left, so that the mouth was oblique, and the right angle of the mouth was lower than the left. The tail movements were normal, and there was no deviation of the tail to one side.

complex type. In those areas which have been mapped out in the dog, the representation of the muscles of the neck exists at *n*, Fig. 148; the fore-limb at *f.l.;* the hind-limb at *h.l.;* face at *f* (see note on Fig. 148); tail at *t;* eye movement at *e.m.;* dilatation of the pupil at *p*. The movements of flexion, extension, and rotation of the various limbs, head, neck, and trunk, and the more complex movements in the higher animals, have each their separate representative in the cortex. The more complex and delicate the movements, the larger the cortical representation, so that the head and arm areas in the ape and man are more largely represented than the trunk and lower limbs, where the movements are of a simpler character. The thumb area is relatively larger than the shoulder or hip area. In Fig. 150 a lesion is shown of the left hemisphere of the dog, involving most of these centres. The symptoms shown are detailed in the description of the figure. In destructive brain lesions it is observed that the muscles, like those of inspiration, which act bilaterally, are not affected by a unilateral lesion. We have previously drawn attention to the fact (p. 150) that the muscles of the larynx have a double representation in the cortex—viz., that both sides are represented in each hemisphere, and the same holds good for the respiratory muscles of the chest and abdomen.*

The motor area of the cerebral cortex of one of the larger herbivora has recently been investigated by Simpson and King.†

These observers have shown that the motor area in the sheep is situated in the superior frontal convolution, and is very limited in extent. This convolution, with the fissures surrounding it, is shown in Fig. 151, while the positions of the motor areas are seen in Fig. 152. The motor area comprises from front to rear centres for (*a*) face, mouth, and tongue; (*b*) head and eyes; (*c*) fore-limb; (*d*) hind-limb. Of these the fore-limb area is the most, and the face area the least, excitable. The hind and fore limb centres are separated by the *splenial sulcus;* stimulation above the sulcus produces flexion and extension of the opposite hind-limb and spreading of the digits. Flexion is always more evident than extension. Stimulation below the sulcus produces movements of the opposite fore-limb, flexion in this case also being more frequent than extension. Where the fore and hind limb areas meet, and extending from the splenial to the *coronal sulcus* (Fig. 151), is an area common to fore and hind limbs, stimulation of which produces movements of the fore and hind limbs of the opposite side, and sometimes of the hind-limb of the same side, but never of the fore. Stimulation of the head and eyes area leads to turning of the head to the opposite side and conjugate deviation of the eyes. The head movement is deliberately performed as though the animal were turning to look at something behind it. Below this area is that found for the face, tongue, and lips, which is relatively the least excitable of all, and its localisation the most uncertain. Stimulation produces lip movements, protrusion and retraction of the tongue, but attempts at mastication were rarely made. In lambs this centre is connected with that of sucking, even to the peculiar tail-movements which accompany the act in this animal. No tail-movements could be evoked from this area apart from sucking.

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* The two-sided representation in each hemisphere is limited to respiration. In other cases each hemisphere causes contraction of chest and abdominal muscles strictly limited to crossed sides, and this is true even of the perineal muscles and *sphincter ani* (Sherrington).

† 'Localisation of the Motor Areas in the Sheep,' Professors Sutherland Simpson and J. L. King, *Quarterly Journal of Experimental Physiology*, vol. iv., No. 1, 1911.

The exposed cerebrum was found, as in other animals, to be deficient in sensation, painful or otherwise; and extirpation of the motor area led to no limb paralysis. The animal walked as well without the superior frontal and middle frontal convolutions as with them. Further, it was quite unaffected as the result of the experimental procedure, and, when liberated, at once began to eat.

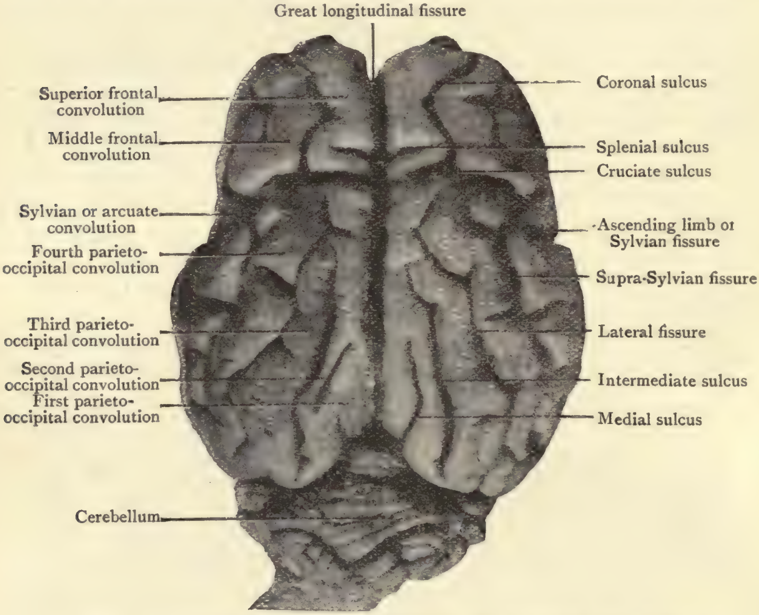
Great longitudinal fissure
Superior frontal convolution
Middle frontal convolution
Sylvian or arcuate convolution
Fourth parieto-occipital convolution
Third parieto-occipital convolution
Second parieto-occipital convolution
First parieto-occipital convolution
Cerebellum
Coronal sulcus
Splenial sulcus
Cruciate sulcus
Ascending limb of Sylvian fissure
Supra-Sylvian fissure
Lateral fissure
Intermediate sulcus
Medial sulcus

FIG. 151.—BRAIN OF SHEEP, DORSAL ASPECT (SIMPSON AND KING).

It seems probable that localisation in the horse does not differ greatly from that of the sheep, or at any rate is nearer to the sheep than that of any other type as yet examined. The remarkable feature is its comparative unimportance, which has long been anticipated clinically (see below). We have already seen that the chief outflow of motor fibres from the brain of the sheep, and presumably of other herbivora, has a subcortical origin from the mid-brain, pons, and medulla (p. 466).

The effect of removing the motor areas differs according to the animal. In the monkey it results in permanent motor paralysis of hand or foot, but not of parts with less skilled movements—*e.g.*, shoulder or knee. In the sheep, as we have just seen, there is no paralysis. In the dog paralysis is not necessarily produced, and it has been supposed that the basal ganglia are capable in this animal of taking on the duties of the cortex. The destruction which has been observed at times in the cortex of the horse is commonly unaccompanied by any symptoms until shortly before death. Colin draws attention to the difficulty in producing paralysis experimentally in the horse from lesions of the hemispheres. Neither the artificial production of a clot in the falciform sinus, nor the introduction of pieces of lead the size of a pea into the convolutions, gave rise to hemiplegia. This quite bears out a frequently observed clinical fact, that it is possible for horses to have tumours the size of an egg in their lateral ventricles without producing any disturbance. The writer has seen several such cases, the tumours being of variable size, and the clinical history has never given more than a few days' illness, though the growths must have been forming for a considerable period.

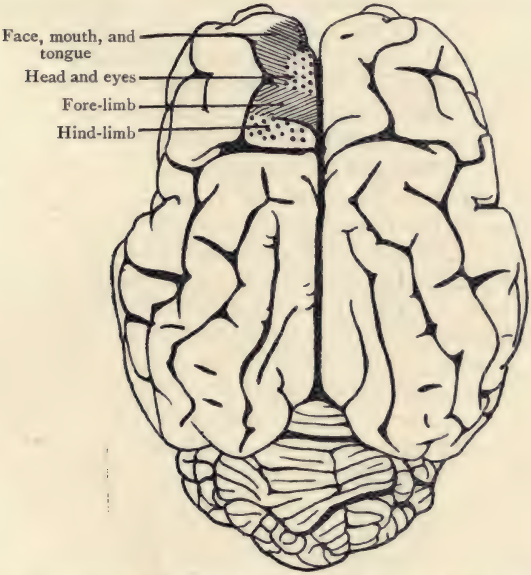

FIG. 152.—DIAGRAM SHOWING POSITION OF MOTOR AREAS ON DORSAL ASPECT, BRAIN OF SHEEP (SIMPSON AND KING).

Strong stimulation of the motor areas produces epilepsy. By observing the groups of muscles first affected and knowing the region of the cortex to which they are related, it is possible, in man, to localise with considerable exactitude the seat of the trouble.

The Sensory Areas.—It will be remembered that these include the higher senses of *vision, smell, taste,* and *hearing,* and the senses of the lower order, *touch, temperature,* and *muscle-sense.* The term 'sensory' is employed in its physiological sense. The seat of pain, we have seen, does not lie in the cerebral cortex. The lower order of senses are those of which we are generally unconscious. Of muscle-sense we are, perhaps, under normal conditions, wholly unconscious ; towards heat and cold the consciousness can be awakened, but is ordinarily unrecognised unless the stimulation is severe. The areas connected with these senses are situated above the crucial sulcus. The *Centre for Vision* is situated in the occipital lobe, and destruction of the centre, say on the right side, is followed by blindness in the two right halves of the retina in those animals where decussation of the optic nerves is incomplete. In those in which it is complete a right-brain lesion leads to a left-eye blindness. We shall deal again with this centre in considering the subject of vision. The *Auditory Centre* has been located in the temporal lobes, and the facts connected with it will be considered in the chapter on Hearing. The auditory and visual centres are capable of eliciting a response in the motor areas, for the ears are pricked, and the head and eyes turned towards an object or a sound, so that connecting paths between the special sense-centres and the regions in the motor area, connected with the muscles in question, are believed to exist. *The Olfactory Centre :* In animals with the sense of smell acutely developed the olfactory bulb and tract are large. The dog, rabbit, horse—in fact, most if not all, of the domestic animals—have the sense of smell highly developed. It is not necessary here to consider the reason in detail, but it is obvious that the whole question of their lives in a natural condition hinges largely on the question of smell ; food, the presence of an enemy, sexual instinct, are capable of exciting in the cortex psychical reactions, which, in the higher animals, are brought about through other channels. In the primitive brain, swellings first develop in connection with smell, and in the process of evolution the cortical centre for smell was one of the first to be established. In the brain with no cerebrum—as, for instance, in the brain of the shark—the olfactory centre, contrary to the general rule in fishes, is immensely developed. Fishes have excellent sight but generally no sense of smell, but the shark lives by the sense of smell, and in the old type of brain with which it is furnished the olfactory nerves spread out into an area of considerable size. In the new type of brain—viz., one with cerebral hemispheres—the olfactory lobes form the principal part of the earlier structures, and in relatively high types of brain, such as are met with in the domestic animals, the olfactory lobes are large and important. In man, who has a poor sense of smell, they have atrophied, and in the whale they have practically disappeared. The cortical centre for smell lies in the region of the hippocampus and temporal lobe, but the central connections of the olfactory apparatus are not fully known. The *Centre for Taste* is ultimately mixed up with that of smell, but its precise locality is unknown. With the *Centre for Speech* we have nothing to do. It is interesting to know that stimulation of the corresponding area in the ape does not lead to the production of voice.

When the sense and motor areas are removed from the cortex, there is a considerable amount of substance left not associated with either of these functions. These have been termed by Flechsig *association areas;* the term *silent areas,* employed by some physiologists in speaking of them, appears especially suitable to veterinary physiology. These association or silent areas are the region of the higher intellectual faculties ; the organs of thought, the region in which impressions conveyed to the sense-centres are interpreted, for it is through the sense centres that intelligence is developed. An association area in the anterior part of the frontal region of man is an important intellectual centre, though of secondary importance to one situated in the parietal region posterior to the fissure of Rolando.

It will be observed that up to this point the functions of the various parts of the cerebrum have been largely determined by direct experiment or pathological observation. This, however, as we indicated previously, is not the only method of inquiry open. Flechsig's embryological method has furnished important results. It will be remembered that it is based on a knowledge of the period at which the fibres in the various tracts acquire their medullary sheath. In the human embryo the nerve-fibres are sheathed three or four months after the axis-cylinder is formed, and the order in which this occurs appears invariable. The afferent fibres are first myelinated, then the efferent, and lastly the association fibres ; this holds good for the nerves of the whole body. At birth the human infant has the afferent system myelinated, but not all the efferent. This, of course, does not apply to those animals which are born with the power of locomotion, but the matter is deeply interesting ; also the fact that the functional activity of nerve tracts is largely dependent on the amount of myelin present. In man the myelination of the fibres of the brain goes on for years after birth, but ceases at forty, and in old age diminishes. We have indicated but briefly the field which awaits the veterinary histologist of the future; in the absence of direct experimental inquiry—which nothing can supplant—important information may be gained by an application of the methods of Flechsig.

Function revealed by Structure.—The development of nervous tissue from its earliest laying down to its maturity has, as we have seen, been turned to account in the interpretation of its function. The next step forward, on somewhat similar lines, was the interpretation of function by a comparison of the structure of the various parts of the cortex in normal and insane persons. Of the structure of the cortex an outline has already been given; the four, or, as some prefer, six, layers of cells and fibres into which this has been divided have received at the hands of Bolton* another classification, which has been generally adopted. It is spoken of as the five-layered type of cortex, and the following are described in man:

1. *Outer fibre lamina:* Two-thirds developed at birth.
2. *Outer cell lamina:* Half developed at birth.
3. *Middle cell lamina:* Three-fourths developed at birth.
4. *Inner fibre lamina:* Two-thirds developed at birth.
5. *Inner cell lamina:* Fully developed at birth.

Watson† has studied the development of these layers in many orders of mammals. He shows that layers 4 and 5 are the earliest to appear, and whether in the highest or lowest mammals there is very little difference in their thickness (Fig. 153). Layer 3 is the next in order of development. Layers 1 and 2 are the last to appear, and the slowest in development. In the lowest mammals layer 2 is generally poorly developed, and even at best obtains but a slight absolute depth as compared with the human brain.

The great difference between the human brain and that of the insectivora lies chiefly in the degree of development of layer 2; whereas, notwithstanding the difference between the brain of man and that of the mole—one of the smallest in the mammalian series—layers 3, 4, and 5 are of much the same thickness (depth) in each animal. Fig. 153 illustrates approximately the relative depths of the cerebral cortical layers in the normal human adult and the mole (after Watson). From the point of view of intelligence, layer 2 is of the utmost importance; it is under-developed to different degrees in idiots and imbeciles, and in chronic and recurrent lunatics the same fact is observed, though in a lesser degree. The examination of the various layers of the cortex in cases of congenital blindness has shown that certain portions of layer 3 are atrophied; this has enabled the cortex to be mapped out into a projection centre for visual impressions, known as the *visuo-sensory area*. At the periphery of this area is another, which can be distinguished by an abrupt modification in the arrangement of the layers. It is known as the

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* 'Further Advances in Physiology,' edited by L. Hill, M.B., F.R.S. Goulstonian Lectures, J. S. Bolton, M.D.: *Brain*, part cxxix., vol. xxxiii., 1910.

† 'The Mammalian Cerebral Cortex, with Special Reference to its Comparative Histology,' G. A. Watson, M.B., C.M., *Archives of Neurology*, vol. iii., 1907.

visuo-psychic, it undergoes no change in congenital blindness, and therefore has no visuo-sensory function. The visuo-psychic layers are not affected in dementia. A third region of the cortex is the *prefrontal*; it is the last to reach maturity, and is the region specially affected in mental disease. Its cell layer, No. 2, has been previously referred to as showing marked retrogressive changes in mental affections. Layer No. 2 is the most important of the human brain, and it is the only one which varies in depth in normal individuals.

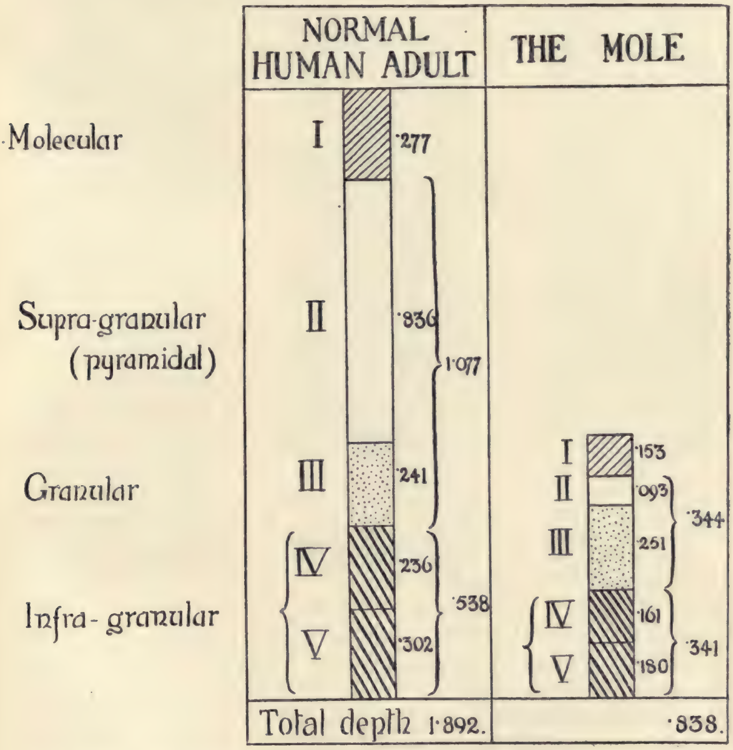
NORMAL HUMAN ADULT
THE MOLE
Molecular
Supra-granular (pyramidal)
Granular
Infra-granular
I
II
III
IV
V
·277
·836
1·077
·241
·236
·538
·302
·153
·093
·344
·251
·161
·341
·180
Total depth 1·892.
·838.

FIG. 153.—THE APPROXIMATE RELATIVE DEPTHS OF THE CEREBRAL CORTICAL LAYERS IN MAN AND THE MOLE (WATSON).

The function of the cell-laminæ of the cortex, according to the observers previously mentioned, and generally accepted by neurologists, is as follows:

Layers 1 *and* 2 carry out the *psychic*, or associational, functions of the cerebrum; they represent educability and general intelligence. Hence they are rudimentary in the insectivora, better developed in rodents, again better developed in ungulates and carnivores than in rodents, and markedly more developed in the primates than the carnivores. They have to do 'with all those activities which it is obvious the animal has acquired (or perfected) by individual experience, and with all the possible modifications of behaviour which may arise in relation to some novel situation ; hence, with what is usually described as indicating intelligent as apart from instinctive acts, the former being not merely accompanied, but controlled, by consciousness ' (Watson). The region of the brain where these processes are carried on is mainly in the prefrontal, or region of higher associations. Of less importance in this respect is the visuo-psychic, or region of lower associations ; and of least importance is the visuo-sensory or projection-sphere region. *Layer* 3 deals with the reception or transformation of afferent impressions, whether from within or without the brain. *Layers* 4 *and* 5 govern the lower voluntary and instinctive activities of the body, which require neither experience nor education. They deal with the preservation and perpetuation of the species, such as food, shelter, and sexual consort, accompanied, though not necessarily controlled, by consciousness. Preservation is deeply, firmly, and early implanted in the brain of the lowest mammals, and in them is as fully developed as in man. It is the common platform on which they meet man. In Fig. 154 is shown the microscopical structure of the Betz-cell area of man and the dog, and the motor area of the pig, the depth of the laminæ in each case being indicated.*

Coverings of the Brain.—The dura mater is a dense fibrous membrane, which acts the part of a protective covering for the brain ; between it and the arachnoid there exists a lymphatic space known as the subdural. The arachnoid contains but few vessels and no nerves, and covers the extremely vascular pia mater ; between the arachnoid and the pia mater is formed the subarachnoid space, which contains the subarachnoid or cerebral fluid.

Cerebral Fluid.—The subarachnoid space communicates with the ventricles of the brain ; the lymph in it is also known to be in communication with the perivascular spaces of the cerebral vessels, and the lymphatic spaces in the perineural covering of nerves. Through the fourth ventricle it communicates with the central canal of the spinal cord, and there is also a connection between the cerebral spaces and those formed on the exterior of the cord. The subdural and to an extent the subarachnoid fluid communicates with the sinuses of the dura mater. The cerebral fluid is secreted by the pia mater and choroid plexus ; in horses it is normally small in quantity, amounting to about 5 or 6 grammes (80 or 90 grains). The use of this fluid is to equalise the pressure on the brain, and to afford protection to the latter ; by the manner in which this organ is suspended inside the skull by the dura mater it is saved from jar and concussion. Both cerebrum and cerebellum half float on water-cushions. Withdrawal of the cerebral fluid leads to convulsions, while an increase in the amount may cause coma, owing to the pressure it exercises. When the arteries in the brain dilate, the skull being unyielding,

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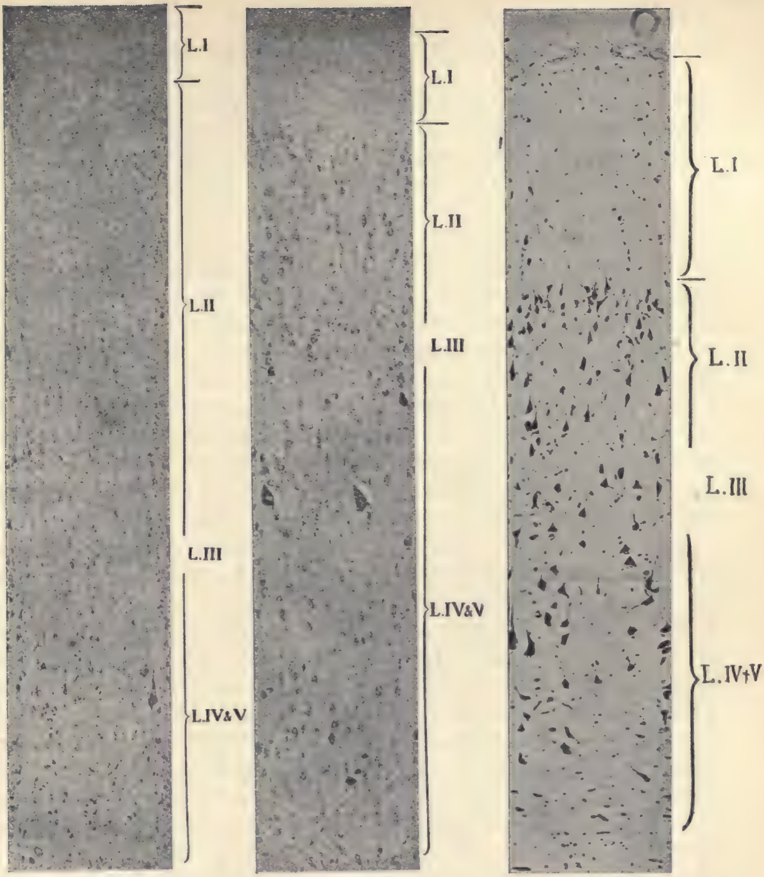
* For these I am indebted to Dr. G. A. Watson. The structure of the cortex of the brain of the pig has not previously been published.



(1) MAN.
× 74 diameters.

(2) DOG.
× 89 diameters.

(3) PIG.
× 109 diameters.

FIG. 154.—CORTEX OF THE BETZ CELL AREA OF MAN AND OF THE CORRESPONDING AREAS IN THE DOG AND PIG (WATSON).

The magnification of (1) is less than that of (2) and (3). The depth of the different layers of the cortex is approximately indicated by the markings to the right of the figure.

In man, L.II.—the pyramidal lamina—is much the best developed layer of the cortex, being considerably deeper than the conjoined layers III. to V. It is the lamina of 'psychic, associative, and educative significance.' In the dog and pig, L.II. is comparatively poorly developed, having a depth of only one-third to one-half of the conjoined layers III. to V. The conjoined layers IV. and V., which are of 'organic and instinctive significance,' are of more nearly equal depth in all three specimens. In this region L.III.—the granule or receptive lamina—is reduced to a minimal depth and distinctness in all the cortices. L.I.—the outer fibre lamina—is relatively deep in the pig, possibly owing to a failure of development, in the upward direction of the pyramidal layer.

The larger cells of L.IV. in the 'motor' area of the pig have not the characteristic shape and appearance of the Betz cells of the human motor cortex; the corresponding cells in the cortex of the dog more nearly approximate to the human type.

In the cortex of the pig the individual nerve cells, though fewer in number than in the dog, have a less embryonic appearance.

some room is made for the extra blood by displacement of the cerebro-spinal fluid.

Movements of the Brain are dealt with at p. 97.

Sleep.

The actual cause of sleep is not known. The tissues require rest and repair, and these are undoubtedly effected during sleep; but no explanation, which has been generally accepted, has accounted for the loss of consciousness which occurs during the process of anabolism. The amount of sleep required by animals appears to be greater in the carnivora than the herbivora. The dog and cat spend a considerable time in this condition of unconsciousness, but the herbivora sleep much less, and for only short periods at a time. Neither class sleep with the same depth nor intensity as man; it is not conceivable that a dog or cat could remain in a condition of profound slumber while considerable noise was occurring. In the case of the horse he is such a light sleeper that the faintest footfall suffices to wake him up. He sleeps with his eyes open or semi-open and on his side, fully extended. The ruminant sleeps with the nose turned in to the side, or resting on the chin, with the head extended. The horse sleeps for short periods together; his immense weight does not admit of his lying for any length of time on one side, for during this period the lower lung does no work and the lower muscles get cramped. He rises and lies on the opposite side, or rolls over to that side; or may rise, eat for a short time, and again lie down. He requires little sleep, but it should be of good quality. Hard-worked horses cannot do without it. The horse has the power of sleeping while standing, for which the limbs are provided with certain necessary mechanisms in connection with the muscles, which will be examined in the chapter on Locomotion. The horse that sleeps while standing drops the head below the level of the withers, the eyelids partly fall over the eyeball, and the limbs are brought rather more under the body than usual. The extensor muscles of the limb cannot be relaxed, or the body would fall; they must accordingly continue to have impulses poured into them in order to maintain their contracted condition. Nor is this confined to the limb muscles; those which sling the body between the fore-legs must also have tone imparted to them if the erect attitude is to be maintained. The impulses dealing with body equilibrium must also continue in operation. None of the mechanisms of the limbs which aid the muscles and tendons are in any way adequate to explain these facts. The extensor muscles, on which everything depends, receive assistance from the fascia of the arm and thigh. The muscles themselves are extremely powerful, and possess in their substance a large amount of tendinous material, such as is evident in all muscles constantly in action ; for example, those of the back, masseter muscles, and others. During sleep the horse is unconscious, and the muscles under no kind of cerebral control, yet they remain strong and in operation without the knowledge of the animal. This is due to the reflex actions of the spinal cord, which, as has previously been urged, are so evident in the herbivora (p. 445) ; likewise the reflex control involving the cerebellum is still in full operation in maintaining posture, so that, asleep or awake, the tonic condition of the muscles is maintained through their agency, not only of the muscles of the limbs, but of those of the back and chest wall, which are equally essential to the maintenance of the erect attitude. The attitude of the sleeping bird, on one leg, is a similar instance of the maintenance of reflex balance when consciousness is in abeyance.

The rest obtained by sleeping in the erect attitude is insufficient for hard-worked horses. They need the complete relaxation of their muscles, and this can only be furnished in the recumbent position. When from anchylosis of the vertebræ or other causes the horse does not lie down, he must be placed in slings at night in order to obtain the needful rest. If not hard worked, they may stand for years without this aid ; on board a ship, or for surgical reasons, they may be kept in a confined position for a considerable period without lying down, if only the muscles be exercised for a few minutes each day. Horses are not free from falling when asleep, they may even actually come to the ground, but this is rare ; what generally happens is that relaxation of the extensors of the fore-limbs occurs, and the animal knuckles over on to the fetlocks and at once recovers itself, but not without inflicting an injury to the skin over the joint. The fall always occurs in front, and not behind ; probably the extra weight on the fore-legs may have something to do with this.

Observations made on man, and those animals which lend themselves to inquiry, show that during sleep the respirations become slower and deeper, and this can readily be observed in the horse. The secretion of urine becomes lessened, the pulse-rate and blood-pressure fall, and the brain shrinks, so that the volume of blood in the other parts of the body is slightly increased, as might be expected from the general inaction of the muscles. The production of carbon dioxide is lessened, while the loss of nervous control over the production of heat causes a fall in temperature. The essential physiological factor in sleep appears to be the anæmia of the brain.

The Theories of Sleep.—The theories formed to account for sleep may shortly be stated. One is based on the *accumulation of acid waste products* in the system ; the source of these lies mainly in the muscles. These tissues, as we have already seen (p. 410), are capable of producing sarcolactic acid. Lactic acid injected into the circulation is said to produce fatigue, and it certainly produces unconsciousness. Sleep after severe muscular work is a necessity, but the acid theory is obviously incomplete, or the idler would need but little sleep. The *doctrine of the neurone* has been evoked to explain sleep, the suggestion being that the synapses in the cells of the cerebral cortex shrink, and in consequence fail to make connection with the incoming fibres from the outside world. Recently the view has been put forward by Salmon* that sleep is presided over by an organ of internal secretion. This, he considers, is furnished by the cells of the cerebral cortex.

Hibernal Sleep.—The long period of sleep enjoyed by hibernating animals appears to be protective in character, and represents the tiding over of a period when food supply is defective. A study of the processes which attend this remarkable phenomenon might be expected to throw some light on the cause of ordinary sleep. It can hardly be urged that in this case the cerebral cells are secreting, a substance, which keeps the animal in a state of such profound sleep that evidences of life have frequently to be carefully looked for. The metabolism occurring during hibernation has been referred to at p. 384. Salmon draws attention to the remarkable activity occurring in the *hibernal gland*. This gland lies beside the thymus, and when stored may reach the whole length of the body. It is highly vascular and charged with a fatty substance, rich in lecithin, which accumulates during the summer and is consumed during the period of sleep, so that at the end of the winter the gland, like the animal, may be a mere shred. This gland contains a colloid substance, and it is significant that a similar material is found in the blood of hibernating animals and in no others. No definite statement can, however, at present be made, as to whether the gland furnishes the sleep-inducing material as well as the food supply.

Psychical Function.—In attempting to define to what extent the faculty of reasoning exists in animals we are treading on distinctly controversial ground. Probably this question can only be positively answered in the affirmative for two animals—viz., the elephant and the dog. With the horse the moral sense† is very small; we do not think he knows he is doing anything wrong when he kicks his stable down once or twice a week, or when he 'runs away,' but he understands that he should not refuse a jump, and a horse careless in his walk or trot knows exactly what every stumble will be followed by, and anticipates matters accordingly. Strength of will most animals lose as the result of domestication. They become mere reflex machines or automata, but there are notable exceptions; for instance, the ass, mule, and occasionally the horse. The so-called stupidity of the ass and provoking obstinacy of the mule are not indications of want of intelligence; on the other hand, they show a determination of purpose and strength of will, which, if more deeply marked and combined with aggressiveness, would keep them as free from civilisation as the zebra. The majority of horses, on the other hand, have no great strength of will; they can be rendered docile and tractable, they will gallop until they drop, work at high pressure when low would suffice, can never apparently learn the obvious lesson that it is the 'willing horse' which suffers, and that the harder they work the more they get to do. All this is due to defective intelligence and a want of the higher faculties; they cannot reason * like the dog or elephant, and are more flexible than the ass or mule. Some horses show signs of reasoning and are capable of grasping a position. A load so heavy as to be beyond the limit of his power, or from some other cause, has taught him to refuse to work; to use the familiar expression, he 'jibs,' he has learned to disobey, he has learned his own strength, and the comparative powerlessness of his master, and this through an exercise of reason. In other words, the horse which refuses to wear himself out in the service of man is one possessing too much intelligence and strength of will for a slave; a 'jibber' is an intelligent and not a stupid horse. As a rule the intelligence and affection of the horse only exist in books and the imagination of those who have the least to do with him; whatever region of the brain affection is located in, it does not occupy much space in the equine. Taking the

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* *British Medical Journal*, July 8, 1911.

† The use of this term is open to objection in the case of animals, but it appears to the writer that something equivalent to the moral sense does

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exist in them. The expression on a dog's face when he has done something he knows to be wrong, or, at any rate, which he knows is against the rules laid down for his life, conveys a conception of the existence of moral sense.

* Exception may be taken to the employment of the term 'reason.' To reason is impossible without general concepts, and in the absence of speech general concepts are difficult to suppose. Nevertheless, the term is convenient, especially as the writer considers that the more intelligent of the lower animals possess what in them amounts to reasoning power.

The absence of speech suggests that animals have no power of intercommunication. The question cannot be discussed here, but those concerned in closely watching the habits of animals must frequently feel that communication between them is not impossible.

dog as the standard to judge by, it may be said with the greatest truth that the large majority of horses have no affection whatever, either for their own kind (excluding maternal affection) or for human beings. There are exceptions, a kind groom is appreciated, and a pair of horses may become greatly attached, or a horse may become very fond of a cat. The liking of mules for the grey mare which leads the troop is well known. Nevertheless, two strange horses cannot as a rule be put together without disagreeing, and no one ever heard of a horse pining away through the prolonged absence of his master. The often-quoted example of a horse jumping over a man on the ground rather than treading on him is an act misunderstood ; it is true the horse jumps over the man, but he does so because he is taught to jump over every obstacle, and the man on the ground might, for all he knows, be a bush. In other words, it becomes largely a reflex, and only to a very limited extent a volitional act. If the leading members of a flock of sheep are made to jump over an obstacle, and the obstacle then be removed, all the succeeding sheep will continue to jump on arriving at the same spot.

If the horse possesses but little affection it is compensated for by cherishing no resentment ; he will kick his friend as readily as a foe, or, in many cases, his groom with as much cheerfulness as a perfect stranger ; to all his hard life and the abominable cruelties of domestication he shows no sign of resentment ; water and feed him, and give him a place to lie in, and he forgets the past in his anxiety for the present. He is a peculiar mixture of courage and cowardice ; physical suffering he can endure, no animal bears pain better ; when his blood is up nothing is too big or too wide for him in the hunting-field, and he has a keen enjoyment for both chase and race in spite of the punishment they may entail. But the same horse is frightened out of his life by a piece of paper blowing across the road, or at his own shadow, and an unusual sight, or a heap of stones on the side of the road has cost many a man his life. No animal is more readily seized with panic, and this spreads amongst a body of horses like an electric shock. Yet panic must not be held to indicate an absence of reason, though the rapidity of its spread in the case of a stampede may suggest it. There are other animals than the horse affected by panic. The dog, with all his intelligence, is acutely affected by a pot tied to his tail, but it does not cause all the dogs he meets to stampede. Panic is not unknown in the highest animal, and reason does not prevent it.

Reasoning power in the majority of horses is very small ; an animal runs away because he is seized with panic, or his spirits are bubbling over. Yet he has sufficient reasoning powers to learn that for the time being he was master of the situation, and if intelligent above the average he becomes a confirmed 'bolter.' Distinct acts of reasoning are rare; of this we daily see examples in our hospitals: horses injured in the most severe manner through their own struggles when placed in a little difficulty, such as a head rope around the leg, or an inability to rise when down, owing to being too close to the wall, or some trifling circumstance of this kind. In these difficulties, if he employed any reasoning powers he would remain quiet until released, instead of which he behaves like a lunatic, inflicting in a short time injuries which may lay him up for months. Or take the case of a horse which gets his tail over the reins when being driven; instead of lifting the tail in response to the exertions of the driver, he draws it closer down to his quarters, gripping the reins as in a vice, and is so astonished and frightened at the new state of things, that he becomes uncontrollable. We can hardly point to a single act in the horse in which the powers of reasoning are clearly brought into play, unless it be that he knows punishment follows refusal to obey, and he often learns to 'jib.' Every horse knows a truss of hay or straw by sight. The point need not be pressed, yet no horse will pass a truss of either lying in the road. He appears unable to reason that what he is familiar with in the stable, may be no more dangerous when met with in an unusual situation.

The horse is very conservative, he likes nothing new or any departure from his ordinary mode of life; he will starve himself for days rather than take a new feeding grain. He will not at first drink out of a trough if he has been used to a bucket or stream, and he dislikes a change of stable or a new place. His gregarious instincts are proverbial; he frets at the absence of his companions, and if used to work amongst a body of horses, as in cavalry, he will take any degree of punishment rather than leave them for five minutes. During the absence of his companions he neighs, sweats, paws with the fore-legs, and almost screams with delight on rejoining them, not because he loves them, but because he dislikes being alone.

The horse has an excellent memory for locality, probably nearly equal to that of the dog or cat; he never forgets a road, and, automaton-like, if he has once stopped at any place on it, he wants to stop at the same place next time, no matter how long the interval may be between the visits. Finally, his predominant feature, and the feature of all animals below adult man, is the childishness present throughout life; probably the absence of care, worry, and anxiety may account for this. The horse will play all day with a piece of rope, or nibble his neighbour persistently; even the oldest horses, when 'fresh,' will perform the antics of a foal, and imitation amongst them is so great that, if one of a string of horses being led along happens to kick out, this repeats itself all along the line as if by preconceived arrangement.

Sydney Smith defined the difference between reason and instinct as follows: 'If, in order to do a certain thing, certain means are adopted to effect it, with a clear and precise notion that these means are subservient to that end, the act is one of reason; if, on the other hand, means are adopted subservient to an end, without there being the least degree of consciousness that these means are subservient to the end, then the act is one of instinct.' Morgan* believes that between instinct on the one hand, and reason on the other, we may insert as a middle term 'intelligence,' while Romanes and others use the word 'intelligence' as synonymous with 'reason.' Morgan defines instinct as a motor response to a certain stimulus—*i.e.*, a reflex act, but one accompanied by consciousness. Animals come into the world endowed with this innate capacity for motor response; but these instincts are not quite perfect; they need training and experience, and their instructor is 'intelligence.' Intelligence, according to this observer, does not imply a conscious knowledge of the relation between the means employed and the end attained; such a conscious knowledge would be reason. In other words we are asked to regard animals as simply reflex machines, their brain being very little higher in the scale than their spinal cord, and for some such a position meets the case, but certainly not for all. If we accept Morgan's definition of instinct and intelligence, it offers no reasonable explanation of why dogs fight, and why they worry cats; why a horse so inclined will turn his quarters towards another as he passes, and rapidly let both hind-legs fly in the direction of his objective; nor will it explain why a horse will use his fore-legs to strike when he knows his hind-legs cannot reach the object of his irritation. It fails completely to explain why an elephant employed piling timber, with human precision, refuses to work one minute beyond the allotted hours. Nor can we believe that the extraordinary sense shown by a sheep-dog is not directed by reason. It is absolutely impossible to believe that such acts imply no conscious knowledge of the relation between the means employed and the end attained.

The higher animals are capable of a limited amount of reasoning; with some it is even relatively well developed, with others it is extremely imperfect. The elephant and dog occupy the top of the scale, the ox and sheep the bottom, the horse comes midway. We do not see how to separate reason from intelligence, but there is no difficulty in separating these from instinct.

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* *Fortnightly Review*, August, 1893.

Some animals are born with such complicated reflex acts as walking, galloping, jumping, etc., so highly developed that they are employed at once. No member of the human family has been seen to walk and run about a few hours after leaving the womb, for both brain and spinal cord are incompletely developed, and the acts have to be learned. This is not so with animals (excepting the dog and cat) : the chick walks out of its shell, foals, calves, lambs, goats, etc., are born prepared to feel their feet at once ; they require no teaching and no imitation, their senses are perfect, they can recognise their mother or a stranger, can see, smell, hear ; in fact, they have nothing to learn, for they are born with as much intelligence as their parents, and only differ from them in one respect, and that is, they are born wild, and so have to learn confidence. Domestication and obedience are not properties transmitted from parent to offspring.

SECTION 7.

The Cranial Nerves.

THERE are twelve pairs of cranial nerves ; of these two only are required to take part in functions other than those connected with the head. This leaves ten pairs, the function of which is wholly connected with the head, either as nerves of special sense, or in a motor or sensory capacity.*

The special senses for which provision is made are *smell, sight, hearing,* and *taste.* Only two of these senses—viz., smell and sight — have nerves exclusively devoted to their function ; both the senses of hearing and taste are furnished by nerves which perform additional functions :

The afferent cranial nerves are :

First, or olfactory.
Second, or optic.
Eighth, or auditory.

The efferent nerves are :

Seventh pair : Motor to the muscles of the face.
Eleventh pair : Motor to the muscles of the neck and shoulders.
Twelfth pair : Motor to the muscles of the tongue.

Mixed nerves :

Third pair Fourth pair Sixth pair	Motor and sensory to the muscles of the eyeball.
Fifth pair Ninth pair Tenth pair	Resemble spinal nerves in consisting of a motor and sensory root, with a ganglion on the latter.

Afferent Group.

The nerves of special sense will be dealt with in the chapter devoted to the Senses.

Efferent Group.

Seventh Pair, or Facial.—This nerve has been grouped as efferent, but in its course it receives sensory fibres, though at its origin it is exclusively motor. It arises from the medulla behind the pons, at the lateral part of the corpus trapezoides. The deep-seated origin is from the facial nucleus in the medulla. In company with the eighth pair, it passes through the internal auditory meatus, but escaping from the internal ear by the aqueduct of Fallopius, it leaves the eighth nerve, and passing beneath the parotid gland, finds its way on to the face, about 1½ inches below the articulation, over the external masseter muscle. During this short course the nerve has supplied the small superficial petrosal nerve, a nerve to the stapedius muscle of the middle ear, and the *chorda tympani*. The latter takes a remarkable course through the petrous temporal bone, supplies fibres to the submaxillary and sublingual glands, and eventually joins the lingual nerve of the glands, there assisting the special nerve of taste. Besides the above branches, the main trunk of the facial, on its way to the face, has supplied motor fibres to the muscles of the external ear, and sensory fibres to the skin of that part; motor fibres to the digastric muscle, to the orbicularis of the eye, and the corrugator of the brow. The main trunk on the surface of the masseter muscle divides into two branches, which between them supply all the muscles of the face, lips, cheek, and nostril with motor power. *The seventh nerve is the nerve of expression.* In this connection it supplies the external ear and all the muscles of the face and lips. Paralysis of this nerve produces a typical facial expression (Fig. 155). The ear droops, the eye remains open, the upper lip is drawn towards the sound side, is elongated and flabby; the lower lip droops, and saliva runs from the mouth; the nostrils are elongated, and the face possesses a stupid, vacant look. Nutritive change may occur to the eye in consequence of exposure, and deafness is present owing to paralysis of the muscle of the middle ear. Bernard pointed out that if both facial nerves be divided in the horse, and the animal galloped, suffocation results in consequence of the nostrils being unable to dilate, and the horse unable to breathe through the mouth. The sensory fibres which join the seventh do so through the *nerve of Wrisberg;* this supplies the mucous membrane of the anterior two-thirds of the tongue. Through the chorda tympani, secretory fibres are

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* The modern system of classifying cranial nerves is described later (p. 522).

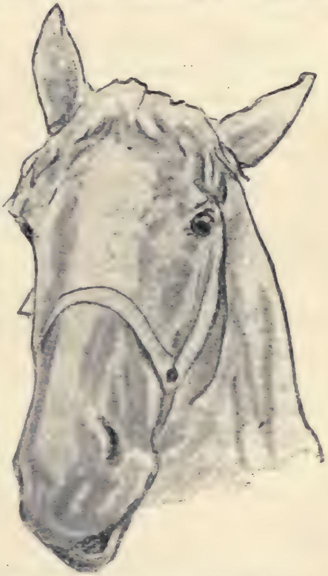

FIG. 155.—CHARACTERISTIC FACIAL EXPRESSION OF THE HORSE WITH PARALYSIS OF THE SEVENTH NERVE.

furnished to the submaxillary and sublingual glands. Though the facial is intimately connected with the masseter muscle, as may be seen in the face of a well-bred horse, no motor fibres are supplied to this, nor, in fact, to any of the principal muscles of mastication, it does, however, supply fibres to the stylo-maxillaris, in part to the digastricus, and to two small muscles connected with the hyoid bone. The seventh pair of nerves in all animals control the muscles of expression, of emotion, pain, and pleasure. In the horse they are in addition respiratory nerves of the first importance, as they control every movement of the nostrils.

Eleventh Pair, or Spinal Accessory.—This is a purely motor nerve, with two roots of origin—viz., the bulb and the spinal cord, as low down as the fifth cervical vertebræ. This latter branch passes up the cord between the motor and sensory roots, receiving filaments on the way, and entering the foramen magnum it joins the root arising from the bulb. In company with the vagus it leaves the skull, then, separating from this nerve, it divides into two branches, which supply the sterno-maxillaris, levator humeri, and trapezius muscles with motor power.

This nerve furnishes motor fibres to the vagus, and is connected with the superior cervical ganglion of the sympathetic. Its course is very remarkable ; having run all the way up the neck within the spinal canal, its dorsal branch passes externally down the neck as far as the upper part of the scapula, and in doing so its object is to innervate the trapezius. It passes by other large muscles of the neck, such as the splenius, without supplying them with any fibres, while all the muscles in the neighbourhood of the trapezius are supplied with motor power direct from the spinal cord.

Owing to its connection with the vagus nerve, division of the accessory causes loss of voice. Bernard showed that crowing in birds was no longer possible after dividing the root within the spinal canal.

The **Twelfth Nerve, Hypoglossal** or **Lingual,** is the motor nerve of the tongue. It is the last cranial nerve to arise from the medulla, which it does by means of several filaments. The deep-seated origin is from the hypoglossal nucleus, which is situated in the floor of the fourth ventricle, near the mid-line. The nuclei of both sides are connected by fibres. On its passage to the tongue this nerve establishes connection with the first cervical and the superior cervical ganglion of the sympathetic, and subsequently supplies all the muscles of the tongue, with fibres to those muscles which depress the larynx.

Mixed Group.

This group, it will be remembered, resembles spinal nerves in consisting of a sensory and motor portion, with a ganglion on the sensory root.

Third Pair, or Motor Oculi.—This nerve has a deep-seated origin in the *anterior corpora quadrigemina* and *peduncles of the cerebrum*. It supplies with motor power all the muscles of the eyeball, including the retractor and muscle of the upper lid, but does not supply the *external rectus* nor the *superior oblique*. Through its connection with the ciliary ganglion it supplies fibres to the sphincter of the iris and the ciliary muscle. At its origin this nerve is connected with the two other motor nerves of the eyeball—viz., the fourth and sixth pairs. Division of the third pair causes the eye to turn downwards and outwards, owing to the unbalanced action of the superior oblique and external rectus muscles. There is also depression of the upper lid, immobility of the eyeball, and dilatation of the pupil. The sense of direction, and the reflex tonus of the eyeball muscles, are also given by these nerves. The movement of the eyeball muscles will be considered in detail later.

Fourth Pair, or Pathetic.—This is the smallest cranial nerve. It arises immediately behind the corpora quadrigemina in the anterior cerebellar peduncle. The deep-seated origin is from a nucleus in the floor of the cerebral aqueduct. Sisson* points out that the fibres of this nerve decussate totally in the anterior medullary velum, so that the fibres for the left eye are derived from the right brain. The fourth cranial nerve supplies only one muscle—viz., the superior oblique of the eyeball.

Sixth Pair, or Abducens.—This nerve arises from the bulb behind the pons, and external to the pyramid. It supplies the external rectus or abductor muscle of the eyeball, the muscle of the third eyelid (membrana nictitans), also the deep recti.

Fifth Pair, or Pars Trigemini.—The large *sensory root* of this nerve arises from the *pons*, close to the *middle peduncle of the cerebellum*, and at the *foramen lacerum* has upon it a large ganglion known as the *Gasserian*. The deep-seated origin of the sensory root is from the *trigeminal nucleus*, which, according to Dexler,† extends from the pons to the sixth cervical segment of the cord, and is known as the *spinal tract of the trigeminus*. The connections of the trigeminal sensory root in the brain are with the thalamus and cerebral cortex of the opposite side. In ungulates it is also, according to Wallenberg,‡ connected with the thalamus of its own side. Further, it is connected with the motor nuclei of the fifth, seventh, ninth, tenth, and twelfth cranial nerves. The Gasserian ganglion behaves like a spinal ganglion. From its axons the sensory fibres arise which pass outwards to the structure of the face and head, and confer on them ordinary, and, in the case of the lips, acute tactile sense. Fibres passing from the Gasserian ganglion to the brain are linked up, as shown above, with the optic thalamus, the central seat of sensory impressions. The *motor root* arises from the *pons* on the inside of the sensory root. From these two roots three branches of nerve are formed—the *ophthalmic*, *superior maxillary*, and *inferior maxillary*. The **Ophthalmic** branch is the smallest, and is purely sensory. It supplies the lachrymal gland, upper eyelid, membrana nictitans, temporal region, mucous membrane of septum nasi, and superior turbinated bone, and provides the sensory root of the ciliary ganglion. The **Superior Maxillary Branch** is of great size, and purely sensory in function. It supplies the septum of the nostril, hard palate, teeth, gums, soft palate, upper lip, guttural pouch, parotid gland, external ear, skin, and other structures of the face. The immense bundle which issues from the infra-orbital canal of the horse is out of all proportion to the extent of tissue to be supplied either with ordinary sensation or with tactile sensibility. The **Inferior Maxillary Branch** is a mixed nerve, its sensory fibres being derived from the Gasserian ganglion, the motor fibres from the the motor root of the main trunk. It is through the motor fibres of this branch that mastication is carried on—in fact, it has been termed the *masticatory nerve*. It supplies all the muscles of mastication excepting the diagastricus. Its sensory fibres are distributed to the lining membrane of the lips and mouth, to the molar and incisor teeth in the lower jaw, and the structures connected therewith, also to the anterior two-thirds of the tongue, to the parotid gland and guttural pouch, to the integument covering the lower half of the head, and to the muscles of mastication. In addition to these extensive functions, the *lingual fibres* not only supply sensation to the tongue, but to the fungiform papillæ, and so assist in the sense of taste.

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* 'Veterinary Anatomy.'

† Sisson, *op. cit.*

‡ Sisson, *op. cit.*

If the fifth pair of nerves be divided, there is complete loss of sensation to one half of the face, part of the ear, cornea, conjunctiva, nasal mucous membrane, and anterior two-thirds of the tongue. There is paralysis of the muscles of mastication, the mouth and tongue become injured by the teeth, in consequence of the loss of sensation ; the food collects on the paralysed side of the mouth ; the cornea ulcerates, either in consequence of the loss of trophic influence, or, as most physiologists think, from irritation caused by foreign bodies, of which the animal has no knowledge, in consequence of sensation being lost. Division of the superior maxillary branch in the horse — known as **Bell's experiment**—prevents the animal from feeding, owing to inability to grasp the food with its lips. Now, as this is a sensory and not a motor nerve, the question arises, Why is the animal prevented from grasping its food ? It is the duty of the sensory branches of the fifth to keep the muscles informed of the position of objects. When sensation is cut off, owing to the entire loss of sensibility in the lips, the animal is unaware how to take hold of the food. It can see the material in the manger, but, in consequence of loss of sensation, does not know how to employ the muscles of the lips to collect it.

There are certain reflex acts in which the sensory branches of the fifth are intimately concerned. When sensation is cut off, the ' feelers ' growing from the orbit are unable to excite the reflex act of closing the eye. Irritation of the Schneiderian membrane produces no sneezing, and irritation of the conjunctiva or cornea does not produce tears ; while the loss of sensation in the tongue fails to stimulate the secretion of saliva.

Ninth Pair, or Glosso-pharyngeal.—This nerve, consisting of a motor and sensory portion, arises by several roots from the anterior and lateral part of the bulb. As it leaves the cranium, a ganglion is found on it—the *ganglion petrosum*. This ganglion is connected with the superior cervical ganglion of the sympathetic and the jugular ganglion of the vagus. There are three branches of nerves distributed from the petrous ganglion : one passes to the *cavity of the tympanum*, and supplies sensory branches to the mucous membrane of the tympanum ; a second is a motor nerve, and supplies the *muscles of the pharynx ;* while the third branch is sensory, and supplies the posterior third of the *mucous membrane of the tongue*, part of the pharynx, and anterior face of the epiglottis. In this branch are taste fibres, which end in the ' taste bulbs ' of the circumvallate papillæ.

Tenth Pair, or Pneumogastric.—This is a mixed nerve, containing motor, sensory, and secretory fibres. There is no nerve possessing such a wide distribution, for its fibres extend from the bulb to the anterior mesenteric ganglion in the abdominal cavity.

The nerve arises from the floor of the fourth ventricle and the nucleus of the solitary tract ; its motor fibres are derived from the spinal accessory. Leaving the bulb, it passes through the *foramen lacerum*, and here the sensory root has a ganglion on it, the *jugular ganglion*. In conjunction with the spinal accessory, the vagus courses its way on to the guttural pouch ; here the two nerves separate. The vagus now joins with the cervical sympathetic, from which results, in the horse and most other animals, a single cord, which passes down the neck in company with the carotid artery. As it enters the chest, the vagus separates from the sympathetic, and the right and left trunks proceed on their way. They both give off important branches known as the 'recurrent laryngeals,' fibres to the heart, trachea, bronchi, and œsophagus, and then each divides into two branches, dorsal and ventral, which come together from opposite sides and form the dorsal and ventral œsophageal branches. These penetrate the diaphragm, after running above and below the œsophagus. The dorsal branch, composed mainly of fibres from the right vagus, passes to the cardia of the stomach, gives off many fibres to that organ, and, continuing its course backwards, joins the anterior mesenteric ganglion (solar plexus) of the sympathetic (Fig. 81). The ventral branch of the œsophageal nerve proceeds to the lesser curvature of the stomach, while fibres pass on to the duodenum and liver. In this way the vagus supplies fibres to the larynx, trachea, bronchi, lungs, heart, œsophagus, stomach, duodenum, liver and, through the sympathetic ganglion, fibres to the small and a portion of the large intestines. In the chapters dealing with the Heart, Circulation, Respiration, and Digestion, the special functions of this nerve have received full consideration. Nevertheless, there are some features of the vagus which may be conveniently dealt with here.

Through the jugular ganglion the vagus is brought into relation with the facial, glosso-pharyngeal and spinal accessory nerves, and it is intimately connected, both in the neck, thorax, and abdominal cavity, with the sympathetic system. In the neck it gives off a *pharyngeal branch*, which forms a plexus with the pharyngeal branch of the ninth pair; and from this plexus motor fibres proceed to the middle and posterior constrictor muscles of the pharynx, and finally distribute themselves on the cervical portion of the œsophagus, to which they furnish motor power. The vagus next gives off the *superior laryngeal*, a mixed nerve, which supplies acute sensation to the mucous membrane of the epiglottis and larynx, and inhibitory fibres to the respiratory centre. It is this nerve which is reflexly excited in the act of coughing, and is capable of arresting inspiration, a very necessary provision at the moment of swallowing. The motor fibres in this nerve are the *external laryngeal*, given off before the main trunk enters the larynx, and supplying motor power to the crico-pharyngeus, crico-thyroid muscles, and in part to the œsophagus. Anatomists are not agreed as to the innervation of the crico-thyroid muscle in the horse. Moeller regards its motor supply as being derived from the first cervical pair;

Chauveau and others, and recently Sisson, described it as being innervated by the external laryngeal nerve. The function of the crico-thyroid muscle being to render the vocal cords tense, division of the nerve produces a hoarse voice. Section of the superior laryngeal causes loss of sensibility in the larynx, and allows food to enter it. The *inferior or recurrent laryngeal* nerves are given off from the vagus within the chest. The right is the first, being given off opposite the second rib, and winding around the dorso-cervical artery from without inwards, while the left is given off above the base of the heart, the nerve winding from without inwards around the posterior aorta. Both nerves leave the thoracic cavity and return up the neck. This complicated arrangement resembles very closely the ' out-of-the-way ' course taken by the spinal accessory in order to reach the trapezius. From the point where each recurrent is given off within the chest their course is not identical; the left, for instance, having a greater distance to travel, is somewhat mixed up with the structures around the base of the heart, while in its passage up the neck it is more superficially placed than the right recurrent. Both nerves supply motor power to all the muscles of the larynx, with the exception of the crico-thyroid. All the fibres in the recurrents are not motor; sensory branches are given off to the trachea and œsophagus in their passage up the neck. At p. 148 sufficient consideration has been devoted to the subject of paralysis of the laryngeal muscles and its influence on respiration. The question is of intense practical interest, owing to the frequency with which the innervation of these muscles is destroyed on the left side. At present there is no satisfactory explanation of this unilateral paralysis. After division of both recurrent nerves, both sides of the larynx are paralysed, and in horses asphyxia is gradually produced. The writer has, however, seen bilateral paralysis not seriously interfering with slow work. In such cases it is believed that the age of the horse is the saving factor; the cartilages, becoming rigid with age, prevent the arytenoids from completely collapsing over the opening of the glottis. If the recurrent nerve on either side of the neck be divided and the horse galloped after the operation, he is found to be a ' roarer.' Not only does paralysis of these muscles interfere with respiration, but it also affects the voice. The altered character of the voice of the horse may be observed either during neighing or coughing. So distinctive, indeed, is the cough of a ' roarer,' that such cases may be at once recognised. Longet found that dividing the recurrent in old animals led to loss of voice, while in the young the voice was rendered unnatural and shrill. This shrill condition was entirely lost by cutting the external laryngeal, which, by paralysing the cricothyroid, prevented the vocal cord from being stretched, and so rendered the animal mute. If the peripheral end of a divided recurrent be stimulated, spasm of the larynx is produced. There are certain vegetable poisons, such as those contained in *Lathyrus sativus*, and others of the Leguminosæ, which appear to especially single out this nerve. Horses fed on grain containing *Lathyrus* are soon rendered incapable of work, as asphyxia occurs through spasm of the larynx.

Chauveau, in his experimental inquiry on the vagus of the horse, found that if both vagi be divided in the neck and the animal fed, the stomach and whole length of the œsophagus frequently became greatly distended with food, in consequence of loss of motor power. It seems certain that the sensation of repletion in these cases is lost, which would account for the animal continuing to eat.

Modern Classification of Cranial Nerves.

The modern conception of the architecture of the cranial nerves is to regard them as built on the same lines as spinal nerves. In this scheme the first and second pairs are not included, the olfactory bulb and retina being regarded as outgrowths from the brain. From the third pair to the twelfth the cranial nerves originate from the brain stem—*i.e.*, the bulb, pons, and mid-brain—which is only an extension forward of the spinal cord. Scattered irregularly in this position, but mainly in the region of the fourth ventricle, are groups of nerve-cells, or nuclei, some of which are sensory, others motor. The motor nuclei are arranged in two longitudinal rows, on either side of the primitive neural axis. From the median row arise the third, fourth, sixth, and twelfth nerves; from the lateral row the motor branches of the fifth, seventh, ninth, tenth, and eleventh.

Nuclei which have been termed sensory are found in the same region connected with the fifth, eighth, ninth, and tenth nerves. These nuclei are the terminations of the sensory cranial nerves, for the latter are arranged in the same way as a spinal nerve, and have a ganglion on their sensory root. The cranial nerves with their ganglia are outside the cranial cavity. The ganglia consist of cells, each, like a spinal nerve ganglion, possessing a **T**-shaped process, one end of which grows to the centre and one to the periphery. It is the central end of the **T**-piece which terminates in the sensory nucleus of the brain stem, by arborising around its cells. It will be observed that the sensory fibres do not arise in the nuclei, but terminate there. The resemblance between the cranial and spinal nerves is completed by the existence of sympathetic fibres in the cranial system.

Under this scheme the sensory portion of the fifth pair represents the dorsal roots of the following motor (ventral) cranial nerves—*i.e.*, seventh and twelfth. The tenth pair becomes the dorsal root of the eleventh. The ninth becomes a dorsal, with no ventral root. The eighth nerve has its dorsal root from the cochlea, and its ventral from the vestibule and semicircular canals.

SECTION 8.

The Sympathetic or Autonomic System of Nerves.

It will have been observed in connection with the cerebro-spinal system of nerves that the bulk of the functions dealt with had reference to the movements of the body and the question of sensation. Excluding entirely the nerves of special sense and the faculties, and speaking generally, the cerebro-spinal system deals with the movement of skeletal muscles and the cutaneous and muscular sensations. It does not touch on the question of the secretion of glands, the movements of the heart and blood-vessels, the movements of the intestines and pelvic viscera, the movements of the body hairs, or the movements of the pupil. It is true that at p. 472 centres were described as existing in the cord regulating some of these functions, but it was made clear at the time that their operations were carried out through the sympathetic system.

The sympathetic system lies outside the cerebro-spinal axis, and if it could be dissected out intact it would be found to consist of a long cord extending from the root of the neck to the sacrum, and studded with nodules, which are the ganglia. This cord is connected in the abdominal region with larger masses of nerve-tissue, also ganglia, which in turn are linked up with microscopic ganglia in far-off tissues. Dissection would show also that it was not possible to remove the system from the body without dividing a series of nerves passing out from the spinal cord, and to which it is attached. Here, then, we have a bird's-eye view of the sympathetic system as a network of fibres and ganglia laid down on definite lines, though irregularly disposed, placed outside the cerebro-spinal axis, yet in direct communication with the spinal cord.

Bearing this arrangement in mind, it is not surprising that the sympathetic is regarded as a distinct nervous system ; it is certainly distinct as regards its function, and it is peculiar in the arrangement of structure ; yet there is nothing from a structural point of view which does not already exist in the spinal system. It is dependent on the cerebro-spinal system for the fibres with which it works, but, having obtained them, it elaborates them into a system peculiar to its own needs, and through its ganglia is enabled, for some of the functions it carries out, to be for the time being independent of the spinal cord. We know, for instance, that the intestines will continue to move when all spinal connections are severed.

The term 'sympathetic' was employed by the earlier physiologists to describe the carrying out of certain 'vegetative' functions of the body, which were not within the knowledge or control of the animal. They employed the term in much the same sense that the word 'reflex' is employed to-day; but the work of Gaskell and Langley has remodelled the entire conception of the sympathetic system, and even changed its name. Langley proposes to call it the **autonomic system,** in order to indicate that it possesses a certain independence of the central nervous system, with power of self-government, and this term is adopted by modern physiologists. It has the further advantage of including certain branches of the cranial nerves, which function as sympathetic, though of cerebral origin. Gaskell divides the sympathetic system into three parts: first, the chain of ganglia running on either side of the spine, closely attached to the arches of the ribs in the thoracic region, and extending back to the sacrum. This he calls the **vertebral** or **lateral ganglia.** The second part of the sympathetic system is that consisting of the large ganglia in front of the vertebræ, in the upright animal, known as **prevertebral ganglia,** and represented by such large masses of nervous tissue as the anterior and posterior mesenteric ganglia; while the third group lies beyond these in the walls of the tissue—for example, the intestines—and is known as **terminal ganglia** (Fig. 157). These three groups are linked together, while the first group is linked up with the spinal cord. Langley has shown that there is no essential difference in function between the vertebral and prevertebral ganglia, but a great difference between these and the terminal ganglia.

The fibres of the autonomic system are mainly efferent, and as derived from the spinal cord are medullated in structure and very narrow. After they have passed through a ganglion they generally lose the medulla, and become non-medullated. In consequence there are white fibres and grey fibres in the autonomic system, depending upon whether they have lost or retained their medullary sheath. There is no difference in the structure of these from similar nerves studied in the cerebrospinal system, with the exception that the fibres are much finer. The ganglia consist of multipolar cells, which do not differ structurally from similar cells met with in the parent system; but their physiology is wholly different. They seem incapable of summation, inhibition, and irreversibility of conduction. It was the presence of multipolar cells which at one time led to the belief that the ganglia of the autonomic system were centres of reflex action. There are no reflex actions in the autonomic system; it is worked as a reflex effect—viz., not under the control of the will—but it has no power to originate reflex functions, because afferent nerves are either absent or under normal conditions blunted in sensibility. Every autonomic fibre must somewhere in its course, and before distribution to its tissue, pass into a ganglion, arborise around a nerve-cell, and from this cell derive its axon, which passes to the tissue concerned. There is no exception to this rule ; it is a fundamental principle in the construction of this peculiar system. Every fibre has therefore a *cell-station ;* it may be in the vertebral, prevertebral, or terminal system. It cannot be in more than one of these, though in the case of those fibres ending in the terminal ganglia they have to pass through the ganglia of the other systems before they reach their destination, but they form no cell connection with them. We are indebted to the labours of Langley for determining the cell-station of the autonomic fibres, which he found could be ascertained by the aid of *nicotine.* This alkaloid has the effect of paralysing nerve-cells, but not nerve-fibres. In order to ascertain whether a nerve-fibre has its cell-station in any given ganglion, it is only necessary to paint the ganglion with nicotine. If the nerve then on stimulation continues to function, it is certain that, though passing through the ganglion, it has no cell-connection with it. A fibre before it makes a cell-connection is known as a **pre-ganglionic** ; after it has made its cell-connection it is termed **post-ganglionic.** Every pre-ganglionic fibre must have originated in the mid-brain, bulb, or cord ; so that every autonomic fibre consists of two neurones, the first lying between the cell of origin in the above tissues and the autonomic ganglion in which its cell-station exists, and the other between the latter and the tissue supplied. In other words, the pre-ganglionic and post-ganglionic fibres represent the two neurones in the autonomic chain, the former being medullated, the latter as a rule non-medullated. The primary division of the autonomic system is into Cranial and Spinal.

Cranial Autonomic System.—It has been stated that there are functions carried out by some branches of the cranial nerves identical in character with those of the sympathetic ; this has led to them being included in the new autonomic system. These nerves are fibres derived from the third, seventh, ninth, tenth, and eleventh pairs. The pre-ganglionic fibres of the **third pair** arise from the mid-brain, the others from the bulb. The cell-station of the third pair lies in the ciliary ganglion ; here the fibres form synapses, and emerge as post-ganglionic fibres in the short ciliary nerves supplying the plain muscle (sphincter) of the iris, and of the ciliary muscle. The pre-ganglionic fibres of the **seventh** and **ninth pairs** have their cell-station in the spheno-palatine, otic, submaxillary, and sublingual ganglia. The post-ganglionic fibres supply dilator fibres to the bloodvessels of the nostril and mouth, and secretory fibres to the submaxillary and sublingual glands. Some fibres of the seventh are distributed with the fifth pair of nerves. The fibres from the **tenth** and **eleventh pairs** of nerves are widely distributed through the vagus. The cell stations are generally unknown, but are believed to be in the tissues concerned. The autonomic fibres of these pairs supply the heart with inhibitory fibres, the muscle of the bronchi with motor power, viscero-motor fibres to the œsophagus, stomach, and small intestines, and secretory fibres for the gastric and pancreatic glands.

Spinal Autonomic System.—This is divided into a thoracic and sacral portion. There are no nerves coming off from the cervical cord which joins the autonomic system. The cervical sympathetic, with its ganglia, is furnished from the thorax. The fibres from the thoracic and sacral portion of the cord which join the sympathetic pass out of the canal by means of the ventral roots of the spinal nerves. They are medullated, white in colour, and are known as the *white rami communicantes*, of which we have previously learnt something (p. 84). One branch is given off at each spinal segment on both sides; this is the *pre-ganglionic* fibre (Fig. 156), and if the account previously given of these has been followed, it is evident that this fibre has now to make its way to a cell-station. For this purpose it leaves the ventral root of the spinal nerve, and joins the *vertebral* ganglia (Fig. 156). Its cell-station may be in the first ganglion of this series with which it meets, and having formed a connection it issues as a *post-ganglionic* fibre (Fig. 157), or it may pass several ganglia before it comes to its own. On the other hand, its cell-station may not be in the vertebral series, and, having passed through, it then, by means of its fibre, seeks its station in the *prevertebral* system (Fig. 157), failing which it passes on to the *terminal* system and finds it there. It is evident that the cell-station of the fibre is connected with its function. If, for instance, the fibres of a vasomotor nerve for the hind-limbs be traced, it is certain that their cell-station will not be in the intestinal wall, but much nearer to the nerves with which they run to their destination—viz., the spinal motor nerves. As a matter of fact, the cell-station for the vasomotor nerves of the hind-limbs and body-wall is in the vertebral ganglia, though not necessarily in the one nearest to the point of issue of the white ramus from the cord. Not only is the vertebral ganglia the cell-station for the nerves supplying the bloodvessels of the hind-limbs and body-wall, but also for the sweat glands and pilomotor fibres of these regions. Nerves for these functions are conveyed by the white ramus to the vertebral ganglia, having, as we have seen, left the ventral spinal root for the purpose. The cell-station having been found, *it* *returns to the ventral spinal root* as a *grey ramus, or post-ganglionic nerve* (Fig. 156), and, with the motor nerve, is distributed to the parts concerned. The vasomotor nerves are mainly constrictor; the fibres for the sweat glands are secretory; those for the hair are motor. The grey ramus does not necessarily return to the same ventral root of the spinal nerve which the white ramus left, but may join the spinal efferent nerves farther backwards. The vasomotor, sweat, and pilomotor fibres for the head and neck do not return as post-ganglionic fibres to the spinal nerve, but are distributed through the cervical sympathetic, and from the superior cervical ganglion are issued to the head as post-ganglionic fibres. The fibres—vasomotor, sweat, and pilomotor—for the fore-limbs also have their cell-station in the stellate ganglion, and from this post-ganglionic fibres are issued. All these details are fully dealt with at pp. 84, 306, and 309. The matter is only referred to here in order to illustrate the principle underlying the distribution of the autonomic fibres, which we are now in a better position to understand.

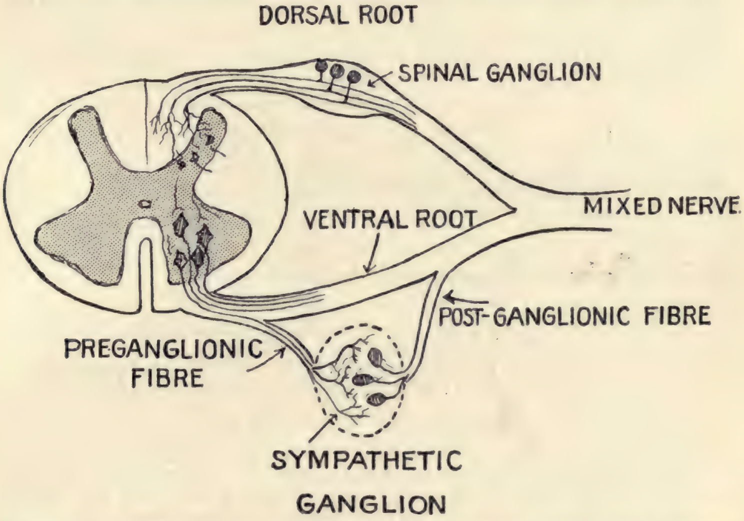

Fig. 156.—Diagram showing the Arrangement of the Dorsal and Ventral Roots of the Cord and the Connection of the White and Grey Rami with the Ventral Root.

The sensory fibres are shown passing through the spinal ganglion and entering the cord through the dorsal root. The motor fibres leave the cord by the ventral root. Shortly after leaving, the white ramus is given off, shown in the diagram as the *pre-ganglionic fibre*. This passes to a lateral (vertebral) ganglion of the sympathetic system, makes a cell connection as shown in the diagram, and issues as a *grey ramus*, or *post-ganglionic fibre*, which rejoins the ventral root.

The bloodvessels, glands, and walls of the abdominal and pelvic viscera are provided with constrictor, secretor, and viscero-motor fibres through fibres from the spinal cord, which pass through the vertebral system of ganglia until they reach the prevertebral, or even the terminal, before they find their cell-station, from which they issue as grey post-ganglionic fibres.

From the sacral cord the pre-ganglionic fibres emerge with the second to the fourth sacral nerves, pass through but do not connect with the vertebral ganglia, but have their cell-stations either in the prevertebral ganglia, hypogastric plexus, or in terminal ganglia in the walls of the viscera. The sacral sympathetic supplies the bloodvessels of the generative organs and rectum with dilator nerves, and the walls of a part of the large intestine and rectum, uterus, bladder, and retractor penis with motor, and, to some of the organs, inhibitory fibres.

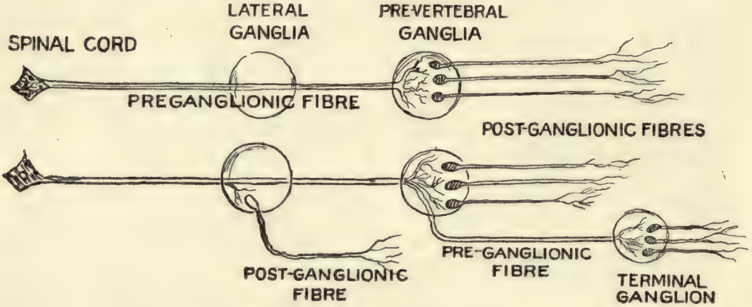

FIG. 157.—DIAGRAM OF THE AUTONOMIC GANGLIA.

The pre-ganglionic fibres issue from the spinal cord, and in the upper figure are shown as passing through, but forming no cell connection with the lateral (vertebral) ganglion. As a pre-ganglionic fibre it continues, and makes a cell connection in the next, or pre-vertebral ganglion, from which the post-ganglionic fibres issue.

In the lower figure some of the pre-ganglionic fibres have formed a cell connection with the lateral ganglion, and issue as post-ganglionic fibres. Others pass through, still as pre-ganglionic, and some of these form cell connections in the pre-vertebral ganglion; others do not, and, continuing as pre-ganglionic fibres, reach the terminal ganglion, where they arborise; from this post-ganglionic fibres issue.

The sympathetic system furnishes impulses of a very opposite nature to the different tissues: for instance, to the bloodvessels, constrictor mainly, but also dilator impulses; to the muscle of the viscera, accelerator and inhibitory impulses. The same branch of nerve, though not the same fibre, may be motor for one organ or tissue, inhibitory for another, constrictor for a bloodvessel, and inhibitory for visceral muscle. All accelerator and inhibitory nerves may be regarded as functioning in the same way as the accelerator and inhibitory nerves of the heart—viz., as anabolic or builders, and katabolic or users up. The cell-stations, generally speaking, of anabolic nerves are in the prevertebral or terminal ganglia ; the cell-stations of the katabolic nerves are, with the same reservation, in the vertebral or else in the prevertebral ganglia.

The *pilomotor nerves* issue from the cord with the ventral roots of the spinal nerves, have their cell-stations in the vertebral ganglia, return to the motor spinal nerve as a grey ramus, and with it are issued to the skin. Stimulation of the grey ramus causes erection of the hair above the vertebra to which it belongs ; stimulation of the white ramus causes erection of hairs over three or four vertebræ.

Sensory Phenomena in the Autonomic System.—It has already been stated that the majority of fibres in the sympathetic system are efferent ; afferent fibres are known to exist, but there is very little information concerning them. As a rule, the parts supplied by the sympathetic system are devoid of ordinary sensibility, so that the existence of afferent fibres must be very limited. The intestines can be handled and cut without the animal evincing pain ; the heart can be injured in many ways, and shows no sign of sensibility ; the liver, spleen, and kidneys are equally devoid of touch sensibility, and ordinarily free from painful impressions. It is the absence of afferent fibres which renders a true reflex action in the autonomic system impossible ; yet stimulation of the central ends of sympathetic nerves gives, as we have seen, great reflex effects on blood pressure, and causes much pain.

It is a remarkable fact that the intestines can be handled, pinched, and douched with hot or cold water, without causing pain. In man the part is not entirely devoid of feeling, but the sensibility is so low that no pain is caused by measures which applied outside the body would cause pain. It is no wonder that the interior of the body is non-existent as a subjective sensation to the majority of people. In spite of this, the most acute pain experienced by the horse is referred to the abdominal cavity. There is no pain to equal that caused by a twisted condition of the intestine, and an attack of acute colic comes next in order of intensity. It is by no means clear why tissues normally insensitive become the seat of such acute pain under disease. This class of pain is not referred to the viscera, but to the abdominal wall, and the explanation which has been offered of this fact is that the sensory cutaneous nerves which are stimulated belong to the segment of cord in which the afferent nerves from the viscera end, and the pain thus referred to the skin.

Flourens observed that the sympathetic ganglia were sensory in different degrees, but always less so than the nerves of the cerebro-spinal system. He frequently noticed that stimulation of the semilunar ganglion of the rabbit caused acute pain, while stimulation of the cervical ganglion was unnoticed. Many observers following Flourens record the same fact regarding the sensory character of the semilunar ganglion when stimulated. Colin, in his observation on the degree of sensibility of the sympathetic ganglia in horses, oxen, dogs, and rabbits, agreed with Flourens that these tissues were endowed with different degrees of sensation, and that the semilunar and thoracic were more sensitive than the upper cervical. He found that the rapidity with which a painful reaction showed itself depended on the strength of the stimulus, weak stimuli taking several seconds before any evidence was given. He also found that if the gastric, splenic, hepatic, and intestinal arteries were pinched with forceps, stretched, or damaged, great pain was shown. These facts enable the pain of colic, and especially intestinal twists, to be explained, though why horses can carry in their intestines stones, sand, gravel, and calculi, week after week and month after month, without causing pain is still unknown.

Pathological.

The absence of alcoholism and syphilis in the lower animals reduces the incidence of nervous affections. It cannot truly be said that worry or anxiety are absent among them, and that hence nervous affections are not so frequent. Nervousness is characteristic of all horses, while if the existence of anxiety is denied the lower creation, one only has to witness what occurs when their young are taken from them. We have seen that the brain is relatively lowly organised in the inferior animals, while the cord is relatively highly organised. Brain trouble is consequently not so frequent as disorders of the cord, but these are known so imperfectly that no useful purpose would be served by attempting their discussion.

CHAPTER XV

THE SENSES

Section I.

Sight.

The delicate structures composing the eye receive a very thorough protection by the anatomical arrangement of the parts. The orbital cavity, for example, is nearly surrounded by incomplete bony walls, and the layers of fat within it assist the muscles in protecting the globe and the optic nerve. The eyelids sweep the cornea and protect the part from dust and exposure ; the tears keep the face of the cornea brilliant ; the *membrana nictitans* removes particles of solid matter which would otherwise produce irritation ; and the eyeball can be retracted to a considerable extent to assist it in withdrawing from injury. The size of the orbit is such that ordinary blows inflicted upon the eye are expended on the margin of the orbital cavity, and not on the eyeball itself, so that the risk of serious injury is far less from large than from small bodies. The shape of the eyeball is not (in the horse) quite spherical : the vertical axis is greater than the horizontal, and the posterior face of the eyeball is distinctly flatter than the anterior.

Structure of the Eye.—Issuing from the back of the eyeball very low down, and inclined to the temporal side of the globe, is the *optic nerve*, which, after describing a peculiar curve upwards, runs in the substance of the retractor muscle to enter the cranium through the optic foramen. This curve in the optic nerve (Fig. 158) is necessitated by the horizontal movements of the eyeball ; when the eye looks backwards, the curve is increased, whereas when it looks forwards the ' slack ' is taken out of the nerve and the curve entirely disappears.

The globe of the eye is anteriorly made up of a transparent convex surface, known as the *cornea*, whilst the remainder of its walls are opaque, and formed by the *sclerotic*, *choroid*, and *retina*. The sclerotic is the tunic on which the strength of the eyeball depends, the choroid may be regarded as that which principally attends to the vascular supply, while the retina is the sensitive expansion of the optic nerve on which the picture is imprinted, and thus gives rise to sensory impressions. The shape and tension of the eyeball is maintained by means of its humours, which are known as the aqueous and vitreous. The *aqueous humour* occupies the space between the cornea and the lens. It is a watery fluid, poor in solids, and is in reality lymph. It is constantly being secreted, probably by the ciliary processes, and as constantly carried away by the lymphatic channels with which it communicates through the spongy *ligamentum pectinatum;* these channels empty themselves into the anterior system of veins. If the anterior chamber be experimentally evacuated, it is refilled in about twenty-four hours. The use of the fluid it contains is to maintain the convexity of the cornea. After death the process of drainage still appears to occur, though, of course, there is no reproduction, the result being that in a day or two the cornea flattens through loss of the aqueous humour.

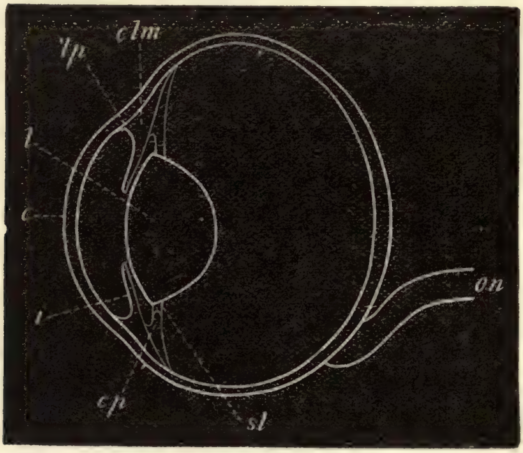

FIG. 158.—VERTICAL SECTION OF THE EYE OF THE HORSE, NATURAL SIZE.

c, Cornea; *l*, lens; *i*, iris; *cp*, ciliary process; *lp*, ligamentum pectinatum; *cl m*, position of ciliary muscle; *sl*, suspensory ligament of lens; *on*, optic nerve, showing its curve. Note its attachment to the lower part of the globe.

The *vitreous humour* is a viscid, tenacious material, contained within the hyaloid membrane, which permeates its substance. The vitreous contains mucin and a very small percentage of solids. The use of this fluid is to maintain the intra-ocular pressure, by which the proper tension of the globe is brought about. The whole of the vitreous chamber is rendered dark by the liberal application of pigment, which covers the inner surface of the choroid coat, with the exception of a surface above the optic nerve, which is brilliant and iridescent in appearance and is known as the *tapetum lucidum.* Between the two humours a diaphragm is situated, known as the *iris*, which regulates the amount of light passing into the eye, and behind this is a focussing arrangement or *lens.* The cornea, lens, and humours constitute the refracting apparatus of the eye. By means of the muscles of the eyeball the globe is given a considerable range of movement, and, in addition, it can be retracted within the orbital cavity. These muscles also afford protection to the optic nerve. In eyes placed laterally the range of vision is considerable. The movements of the head are of even more importance than the movements of the eyeball muscles in securing a wide range of vision.

The similarity in construction between the eye and the apparatus known as a camera is very marked ; both have a refracting surface placed anteriorly, a diaphragm to cut off superfluous rays of light, an arrangement for focussing, and a dark chamber in which a sensitised surface is placed, and on which a reduced and inverted image of the picture is impressed.

The **Cornea** in most animals is circular in outline ; in the horse it is somewhat oval. When viewed from the front and divided into two halves by a vertical line, it is distinctly larger on its nasal than on its temporal side. It is a very tough, non-vascular membrane, richly supplied with nerves, and nourished by lymph which circulates freely in it. It may be regarded as the chief refractive apparatus of the eye. When viewed from the side, the cornea is seen to be convex. Measurement shows that in the majority of horses the curvature of the cornea taken in its horizontal and vertical meridians is not exactly the same, which it would be supposing its surface were accurately spherical. The excess of curvature of one meridian of the cornea over that of the surface at right angles to it produces a defect in vision which is known as **astigmatism.** The meridian in the horse which is nearly always the flattest is the horizontal.

The **Lens** is composed of various onion-like layers of different refractive powers. In shape it is bi-convex, the convexity of its posterior face being greater than that of the anterior. It is held in its place by a capsule which really suspends the lens in the eye, the capsule receiving attachment to some long processes behind the iris known as the *ciliary processes.* In the horse the lens is in contact with the ciliary processes ; in most other animals there is a small space between the two. The lens possesses inherent elasticity, which admits of its surface undergoing an alteration in shape, so as to be flatter at one time, more convex at another. This alteration in shape occurs through the ready manner in which the lens, by its elasticity, yields to the pressure exercised on it through its capsule, so that if the tension of the capsule be relaxed the lens bulges, or if the tension be increased it flattens. In this way the eye is focussed or accommodated to various distances, a subject which will be dealt with presently.

The **Iris** is a curtain with a hole in the centre, called the *pupil*. The shape of the pupil varies in different animals. In the dog it is circular ; in the horse, sheep, ox, and cat elliptical. In the latter animal the elliptical slit is placed vertically ; in the others horizontally. Berlin, whose work will be referred to presently, regarded the horizontal pupil as increasing the distinctness of the retinal image. Both in the horse and cat, according to this observer, the direction of the pupil corresponds to the least curved meridian of the cornea. The iris is mainly a collection of bloodvessels and muscular fibres, the whole being heavily coated with a brown pigment in the horse, though occasionally this is wanting, giving it a bluish - white streaky appearance, as in the so-called 'wall-eyed' horse. In the ox and dog the iris is a brighter brown than in the horse, while in the sheep it is brownish-yellow. The muscular fibres of the iris are of the unstriped variety, and disposed in a circular and radiating manner. A contraction of the circular muscle contracts the pupillary opening ; a contraction of the radiating fibres dilates it. On bleaching the iris of the horse the disposition of its muscular fibres can be easily studied. Fig. 159 shows the peculiar wrinkles in the curtain and pleats in the iris above and below the pupil, caused by the radiating fibres. Immediately surrounding the pupillary opening is a circular layer of muscular fibre. The wrinkles and pleats in the iris of the horse are confined to its anterior face ; the surface next the lens is perfectly smooth. Langley and Anderson, from their observations on the cat, dog, and rabbit, proved that a dilator muscle to the iris exists. This question was for a long time in dispute. It is now accepted that dilatation of the pupil is due to the

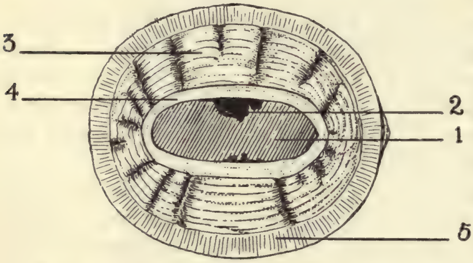

FIG. 159.—BLEACHED IRIS OF THE HORSE.

1, Pupillary opening ; 2, corpus nigrum ; 3, iris showing wrinkles and pleats in its structure ; 4, circular muscle surrounding the pupillary opening ; 5, *Ligamentum pectinatum.*

contraction of the dilator muscle and inhibition of the circular muscle.

The nerve supply to the two muscles of the iris is not the same; the circular fibres are supplied with motor power through the third cranial nerve, whilst the dilator muscle is supplied by the sympathetic. The latter fibres arise in the mid-brain, run down the cord, and terminate in cells in the lower cervical region. Here fresh neurones arise which emerge from the spinal cord at the eighth cervical and first three thoracic spinal nerves, from a part known as the cilio-spinal centre; they travel up the neck in the cervical sympathetic, connect with the superior cervical ganglion, thence to the Gasserian ganglion, and by means of the long ciliary nerves in the ophthalmic branch of the fifth nerve they reach the iris. The fibres of the third nerve connect with the ciliary ganglion, and by means of the short ciliary nerves (post-ganglionic fibres, now autonomic) they reach the iris. If the third nerve be divided, the radiating muscular fibres of the iris contract under the unbalanced action of the sympathetic, and thus dilate the pupil; if the sympathetic be divided, the pupil contracts under the unbalanced action of the sphincter fibres. Under ordinary conditions both constrictor and dilator muscles are receiving impulses, which neutralise each other, so that the iris is readily responsive to any excess of impulses which disturb the balance. This act is a true reflex, being carried out through the afferent fibres of the optic nerve, a centre in the brain probably situated in the floor of the aqueduct of Sylvius, and an efferent path furnished by the third pair of nerves. Stimulation of the retina by light is the natural method by which alterations in the size of the pupil are brought about; in a brilliant light the pupil contracts, in a low light it dilates. In the horse this is not strictly true; in direct sunlight the pupil of this animal is a mere narrow chink, but in ordinary diffused daylight it barely responds, or if it does contract it is so little as not materially to reduce the size of the pupil. Even when light is concentrated on the eye, either by means of a mirror or a lens, the iris practically remains unchanged. Under the influence of artificial light it actually dilates. In all herbivora the pupil is relatively sluggish in response to the stimulus of light. The contraction is greater in the exposed than in the opposite eye. Harris,* indeed, regards this fact as an indication of a low standard of visual acuity in the herbivora. In the cat the reaction of the pupil is brisk, and sharper than in the case of the dog. The above observer considers that want of visual acuity is compensated in the herbivora by greater keenness of hearing and smell. They are animals which are hunted, instead of hunting. Hearing and smell give earlier indications of approaching danger than sight.

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* 'Binocular and Stereoscopic Vision in Man and Other Vertebrates.' W. Harris, M.D., M.R.C.P.; *Brain*, part iv., 1904.

As the pupil of the horse dilates under artificial light, the fact is taken advantage of in ophthalmoscopic work, and the use of atropine rendered unnecessary. There are certain drugs which dilate the pupil, such as atropine and cocaine, and others which contract it—for example, morphine and eserine. Dilatation of the pupil is spoken of as *mydriasis*, and contraction as myosis ~~*miosis*~~. Atropine and cocaine are therefore termed *mydriatics*, and their antagonists myotics ~~*miotics*~~. It is believed that atropine acts by paralysing the constrictor fibres furnished by the third pair. In greater strength the fibres supplying the ciliary muscle may also be paralysed, and the animal unable to use the eyes for close vision. All animals, however, are not so affected. The ciliary muscle of the horse is not paralysed by atropine. It is curious to observe in the horse that, although the pupil when normally contracted is elliptical, yet when dilated it becomes circular. The chief radiating fibres are above and below, and but very few at the sides. Eversbusch* has studied the structure of the iris of the horse, and states that the elongated form of the pupil is due to the presence of an accessory apparatus on the posterior surface of the iris, which he calls the *ligamentum inhibitorium*. Through this ligament the sides of the iris are not pulled in by the contraction of the sphincter muscle.

The long axis of the pupil in the horse is always horizontal, or practically so, no matter what the position of the head may be. This is a point which will be touched on again in dealing with the muscles of the eyeball. The pupil of the horse dilates moderately after the animal has been galloped. *Immediately* after a violent death it dilates widely, but in the course of twenty-four hours or so it gradually contracts until the pupil becomes a mere slit. In the horse there exists on the edge of the iris, at the centre and upper part of the pupil, one or more large soot-like bodies, known as **corpora nigra** (Fig. 159). A small one may be found on the lower margin of the iris, but the upper are the most prominent. When the pupil is strongly contracted in direct sunlight, the centre of it is entirely blocked out by these pigmentary masses, and divided into an inner and outer portion. It would appear as if this might cause an imperfect image to be imprinted on the retina; but on subjecting the question to actual experiment, no broken image was found to result from the use of a diaphragm the centre of which was blocked out. The use of these bodies is doubtless to assist in absorbing rays of light, but their position in the centre of the pupil would not appear theoretically to be the most suitable position, and they must have some other function. The horse, as far as we know, is the only animal possessing them.

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* *Zeitschrift für Vergleichende Augenheilkunde*, Heft 1, 1882.

Ligamentum Pectinatum.—Around the attached margin of the iris—viz., at the corneo-scleral border—a peculiar spongy tissue exists, which gives the iris at this part a distinctly elevated rim; this is known as the ligamentum pectinatum (Fig. 159). Roughly speaking, it is a rim of spongy iris traversed by canals, crevices, and spaces, which lead into the lymphatic system of the eye. The function of this tissue is to carry off the aqueous humour as rapidly as it is worn out and replaced, by which means the normal tension of the anterior chamber is maintained.

Intra-ocular Pressure has been estimated at 25 mm. of mercury. This condition of tension is a necessary factor in keeping the various structures of the eye in position, while an increase above the normal leads to rapid destruction of vision.

The **Choroid Coat** contains the vessels which nourish the retina; it possesses innumerable nerves, numerous lymphatics, and, further, it is an elastic coat. At its anterior part, behind the iris, it forms the peculiar folded structure known as the **Ciliary processes,** and in front of this it furnishes the tissue which is called the **Iris**; the iris and ciliary processes are therefore part of the choroid coat. With the exception of one area, the whole of the interior of the choroid is covered with pigment, and the same extends on to the processes and iris. The area which is an exception lies on the posterior wall of the eyeball above the optic nerve; it is of a brilliant colour, being a mixture of green, yellow, and blue, and is known as the **tapetum lucidum** (Plate I., Fig. 4*). This is found in both herbivora and carnivora; in the former it is due to the interference of light causing iridescence, produced by the arrangement of the connective-tissue fibres of the choroid, and not to the presence of any pigment; in carnivora it is due to minute crystals in the cells of the part, the crystals causing the interference. The use of the tapetum is generally supposed to enable animals to see in the dark; this, of course, is impossible, but it is probable that its presence enables an animal to see better in a dim light.

The **Ciliary Zone** is a peculiar and important part of the eye, formed on the one hand by the junction of the cornea and sclerotic, and on the other by the iris and ciliary processes. Between these lies a muscle known as the ciliary, which is firmly attached to the corneo-scleral margin, and runs backwards into the choroid, where it is attached. In man the

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* Berlin, *Zeitschrift für Vergleichende Augenheikunde,* Heft 2, 1882.

ciliary muscle consists of both circular and longitudinal (or meridional) fibres ; in the horse, and probably all the lower animals, only meridional fibres exist. The muscle is composed of unstriped fibres, is innervated by the third pair of nerves, and its use is to pull the choroid forward. The object of this will be apparent when the question of accommodation is discussed.

The **Vitreous** humour is enclosed in the hyaloid membrane. Anteriorly this membrane, here known as the *zonule of Zinn*, becomes dovetailed into the ridges formed by the ciliary processes, and, enveloping the lens, forms its *suspensory ligament.* If the amount of vitreous humour present is sufficient in quantity, this ligament of the lens must always be tense, and as it is very inelastic, it tends to keep the lens flattened. The matter will be referred to again in speaking of accommodation.

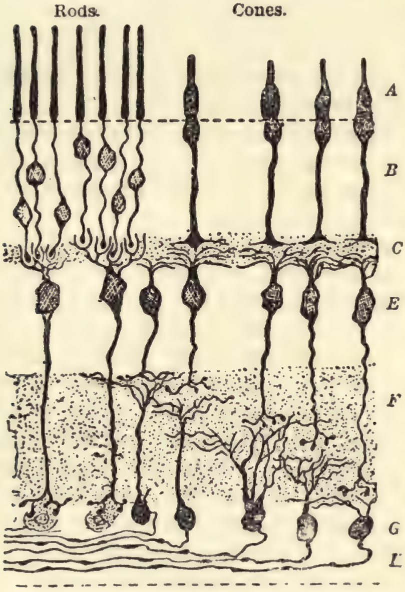

Fig. 160.—Diagram of Structure of Retina (Bowditch, after Cajal).

A, Layer of rods and cones ; *B*, external nuclear layer ; *C*, external molecular layer ; *E*, internal nuclear layer ; *F*, internal molecular layer ; *G*, layer of ganglion cells ; *H*, layer of nerve fibres.

The **Retina** lies within the choroid and outside the vitreous humour ; it spreads out from the entrance of the optic nerve of which it is the expansion. Microscopic examination shows this membrane to be composed of seven layers (Fig. 160), of which the most important is one termed from its appearance the layer of rods and cones. It has been shown conclusively that these rods and cones are the essential elements of the retina, and that wherever they are absent the part is insensitive to light, as, for example, at the entrance of the optic nerve which forms the *blind spot.* Though the layer of rods and cones is the most important, it is not placed, as one would suppose, next the vitreous humour, but next to the choroid, whilst the layer next to the vitreous humour is composed of nerve fibres and ganglion cells. Rays of light have, therefore, in the first place to pierce the entire thickness of the retina in order to arrive at the rods and cones. Here they give rise to a nervous impulse which retraces its steps in the retina, until it arrives at the layers next the vitreous humour, from which it is carried off by the optic nerve to the brain. It is in the rods and cones that the primary conversion of light-vibrations into visual impulses is effected. Each cone is connected with a single nerve cell, but there may be several rods to one nerve cell ; the cone is, therefore, considered to offer a more direct conducting path than the rod. In the human eye cones exist over the area of acute vision. Cones are especially adapted for daylight vision (see p. 561) ; further, it is believed they are the seat of colour perception.

Visual Purple, or *Rhodopsin*, is a curious red pigment existing in the retina ; it is found in the rods, but not in the cones. This colouring matter is readily decomposed by light, and is consequently always being produced. Its function in connection with the theory of vision is considered at p. 561.

Optic Disc.—The entrance of the optic nerve within the eyeball is spoken of as the *optic disc* or *papilla ;* it is a concave oval surface, measuring in the horse 3·5 mm. deep and 5 mm. wide, surrounded by a white ring formed of sclerotic (see Plate I., Fig. 4). It lies, in the horse, towards the bottom of the eyeball and inclined to the temporal side. This region is blind, owing to the absence of both rods and cones. On the temporal side of the optic disc in man and the higher apes is a yellow area, the *macula lutea* or *yellow spot*, which is about 6 mm. in diameter. It is now believed that the yellow tint of this area is a post-mortem change, for it cannot be seen in the living eye. Within the yellow spot is a small depression, known as the *fovea centralis*, having a diameter of 0·3 to 0·4 mm. At this point the retina is thinned out until nothing but the cones are left. This is the area of acute vision, and it is situated in the centre of the field of vision. Visual acuity diminishes rapidly as the image falls away from the fovea. There is no yellow spot or fovea centralis in the lower animals, but there is, no doubt, a region where vision is most acute. Most animals raise the head when staring intently at an object. This is especially well seen in the horse, who, by raising the head very high and protruding the muzzle, renders the face more horizontal, and doubtless brings the object on to the most receptive part of the retina. In man a line drawn from the yellow spot to the centre of the cornea is called the *visual axis* of the eye. The visual axis does not agree with the *optic axis*—viz., a line drawn exactly through the centre of curvature of each refractive medium.

The **Optic Nerve** arises from the retina, and the first portion of its path ends by forming synapses with the cells in the external geniculate body, the posterior portion of the optic thalamus, and the anterior corpus quadrigeminum. The most characteristic naked-eye feature in connection with the nerves is the fusion which occurs. The nerves from the two eyes meet on the base of the brain, and form what is known as the *optic chiasma.* They again separate and pass to their respective sides of the brain. This crossing of the optic nerves is a question of great importance, and whether the crossing is complete or incomplete depends upon the animal and the type of eye. In fishes the nerves cross and remain quite distinct: one may even pass through a slit in the other, but neither gives fibres to the other. In birds the fibres meet, interlace, alternate, but the decussation is complete —viz., the fibres of the right eye all pass to the left brain, and *vice versa.* The law, in fact, regarding the decussation of the fibres of the optic nerve is that in all vertebrates below mammals—*i.e.*, in fishes, amphibia, reptiles, and birds—there is total decussation. In all animals higher than these decussation is incomplete; at first only a small number, and gradually, as monkeys and man are approached, a considerable number of fibres pass from the retina to the same side of the brain. In the horse one-sixth of the fibres are said to be direct, in man three-fifths.

The question of decussating and direct fibres hinges largely, if not entirely, on the position of the eyes in the animal's head. When, for instance, the eyes are laterally placed, and any attempt to look forward is out of the question, decussation is complete; but as a certain amount of forward as well as lateral vision becomes established, a proportion of direct fibres in the nerve occurs, until at last the animal with perfect forward and imperfect lateral vision is reached, when more than half of the fibres are direct. Nor is this a coincidence; on the other hand, it is intimately connected with the question of the visual path, which has been traced into the higher regions of the brain.

In fishes the full extent of the visual path is reached at the mid-brain, as these animals possess no cerebrum; but as the scale is ascended, and the cortical centres develop, the visual path extends upward from the mid-brain to the cerebrum, where, in its occipital portion, a visual region arises, fibres from the external geniculate body being projected on to the occipital lobe. Here we meet with another example of the unity of type of the nervous system. The first neurone exists between the retina and the mid-brain, the optic fibres being axons of the nerve cells of the retina. By synapses these are connected with a second neurone running from mid-brain to cerebral cortex. The area connected with vision in the higher mammals can be accurately mapped in the *calcarine fissure* of the occipital lobe by following a white line, which can be readily traced, known as the *line of Gennari.* This line is a layer of nerve fibres of a special kind, lying midway between the surface and the white matter of the brain. The area thus mapped out is the **visuo-sensory area**, of which something has been said at p. 500. Mott has described the visual cortex of insectivora, rodents, marsupials, ungulates, carnivora, lemurs, and primates,* and points out that the more the animal depends on vision as a directive faculty in its preservation, the more complex the structure of the visual cortex becomes. For example, in the *mole and shrew*, who are probably only able to perceive light from darkness, the cell structure of the visual cortex consists almost entirely of granular-like small stellate cells ; below this is a thin layer of polymorph cells, and there occasional large pyramidal-shaped cells occur. In the *hedgehog* the cells are more complex, but the type of cell-lamination is simple.

In *rodents* the visual cortex is becoming more complex, and in the rabbit there are large stellate and branching pyramidal cells, and a well-marked line of Gennari. In *ungulates* the cell lamination exhibits a relatively deep polymorph layer, numerous solitary cells of Meynert, large and small stellate cells, a fair number of cells corresponding to the pyramidal layer, and a well-marked line of Gennari. In *caninæ* there is an extensive area of visual cortex, and in addition to the layers common to the orders described, it has a fair depth of pyramidals. In *felidæ* the striking feature is the depth of the pyramidal layer, the solitary cells of Meynert are numerous, and the polymorph layer relatively diminished.

On to the visuo-sensory area the retinas are projected by means of the occipito-thalamic fibres ; but the impulses received are not there analysed. Conscious visual sensations, and especially visual associations and memories, are developed in the **visuo-psychic area**, and this, as Mott has shown, is distinguished by the presence of many small and medium-sized pyramidal cells in its outer layers, and the absence of the line of Gennari. The visuo-psychic area in animals is structurally not nearly so distinct as in man.

Watson, whose work on the structure of the cerebral cortex of animals has been referred to at p. 502, considers that the visual area in ungulates and carnivora has not the definite appearance of a projection sphere ; he believes that in the lowest mammals vision has not a very definite higher cortical representation.†

In animals with binocular stereoscopic vision the right occipital cortex receives the visual impression from the two right halves of the retinas, the left occipital lobe impressions from the two left halves of each retina. In animals where the eyes are laterally situated and binocular vision impossible, the visuo-sensory area receives a picture from the opposite eye, and from that only, so that two different pictures are implanted at one and the same time on the right and left cortical visuo-sensory areas of such animals.

The Ophthalmoscope.—In order to examine the structures posterior to the iris, a mirror with a hole in the centre is applied to the eye of the observer, so that he can see through the hole into the observed eye ; from a suitable source of light rays are reflected by the mirror through the pupil on to the retina to be examined. When light is thrown into the eye, the rays are reflected back through the pupil in the direction in which they entered, and pass through the hole in the mirror into the eye of the observer. On looking at the retina of the horse, a brilliantly coloured surface is seen illuminated, the tints being a mixture of yellow, green, and blue, studded with minute dots ; this coloured area is the tapetum (Plate I., Fig. 4). Examination shows this surface to be situated above the optic disc or papilla ; the optic papilla appears of a pinkish colour, with a slightly raised whitish margin. The fundus is a beautiful object, but very difficult to study in the eye of the horse, owing to its frequent movement, so that only occasional glimpses of the papilla can be obtained. From the optic papilla a dense network of vessels may be seen radiating, but extending no great distance from it ; this is characteristic of the retina of the horse. The remainder of the fundus is purple or brown, but owing to its extent very little of it can be seen. In other animals the vessels radiating from the disc are wider apart and more regular, and several of them have received names ; moreover, the arteries can be distinguished from the veins, which is not possible in the horse. It is to be borne in mind that the view thus obtained of the fundus of the eye is a magnified image, both the lens and vitreous humour making it appear about three times larger than normal. Owing to the presence of the tapetum in the horse, a perfect examination of the lens and fundus may be made without the aid of artificial light ; while under the influence of artificial light the pupil dilates so much that there is no need for the use of atropine.

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* 'The Progressive Evolution of the Structure and Functions of the Visual Cortex in Mammalia.' *Archives of Neurology*, vol. iii., 1907. F. W. Mott, M.D., F.R.S.

† 'The Mammalian Cerebral Cortex, with Special Reference to its Comparative Histology.' *Archives of Neurology*, vol. iii., 1907. G. A. Watson, M.B., C.M.

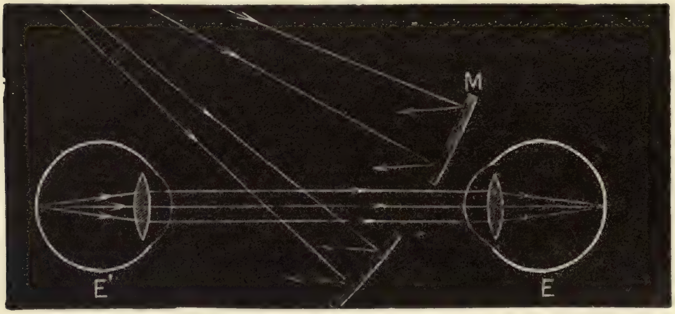

FIG. 161.—DIRECT METHOD OF USING THE OPHTHALMOSCOPE (STEWART).

Light falling on the perforated concave mirror M passes into the observed eye E′ ; and, both E′ and the observing eye E being supposed emmetropic and unaccommodated, an erect virtual image of the illuminated retina of E′ is seen by E.

Accommodation.—All rays of light proceeding from a distant object may be regarded as parallel, and all those proceeding from an object within 6 metres (20 feet) of the eye may be regarded as divergent. A distant object is one situated anywhere between 20 feet from the eye and infinity ; an object closer than 20 feet to the eye is called near, and this point increases up to 10 to 13 centimetres (4 or 5 inches), at which distance no object can any longer be distinctly seen. The nearest distance at which objects can be distinctly seen is called the *near point.* Parallel rays need no focussing on the retina other than that provided by the cornea ; but rays from near objects require focussing owing to their divergent nature, and it is evident that the nearer the object to the eye the greater the focussing required.

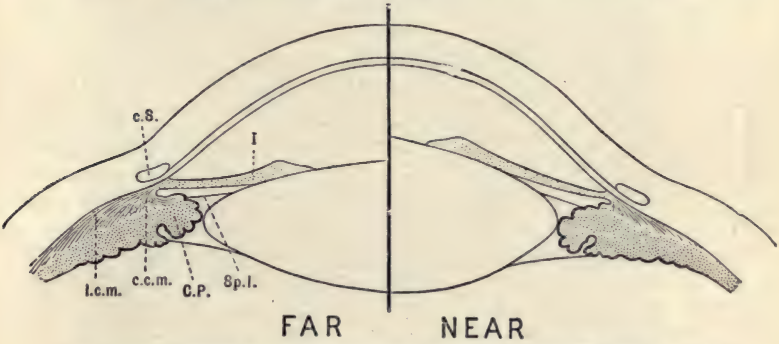

FIG. 162.—DIAGRAM TO ILLUSTRATE ACCOMMODATION (FOSTER, AFTER HELMHOLTZ).

C.P., Ciliary process ; I, iris ; Sp. l., suspensory ligament ; l.c.m., longitudinal ciliary muscle ; c.c.m., circular ciliary muscle ; c.S., canal of Schlemm. The left half represents the shape of the lens for viewing distant objects, and the right half that for viewing near objects.

This focussing is brought about by a change in the shape of the anterior surface of the lens ; it becomes more convex for near objects, and this increase in convexity is due to the ciliary muscle drawing forward the choroid coat, and with it the ciliary processes. By this means the tension normally exercised through the zonule of Zinn (the suspensory ligament of the lens) is relaxed, and the lens of its own inherent elasticity bulges forward, and so increases the curvature of its anterior face (Fig. 162). A more convex lens is a more convergent one, and its focus is therefore shorter ; in this way the images of near objects are brought to a focus on the retina and distinctly seen, whereas if this increase in curvature had not taken place, the image would have been focussed behind the retina. The power the eye possesses of focussing itself is known as the mechanism of accommodation, and the explanation given above is that of Helmholtz; it is the one generally accepted.

When a candle is held opposite to the eye three images of the flame are seen: one, a very sharp bright one, obviously reflected from the cornea; a second, much duller, but also large, reflected from the anterior surface of the lens; and a third, very small, brighter than the middle one, and *inverted*, reflected from the posterior surface of the lens (Fig. 163). In a normal eye these are seen perfectly, and move in a definite direction when the candle is moved, the inverted image passing in an opposite direction to the two erect images, and all are equally visible at any point on the reflecting surfaces. This phenomenon has been taken advantage of in determining the clearness of the media of the eye, and though superseded by the greater accuracy of the ophthalmoscope, it is still a valuable aid; in cataract one or more of the reflections becomes blurred, and sometimes the image is duplicated. The first and second images are erect, inasmuch as they are reflected from a convex surface, but the third image is inverted, being reflected from the posterior surface of the lens, which, viewed from the front, is concave. During the act of accommodation the relative position of these images alters; the second becomes smaller or larger, and advances nearer to or recedes from the first, as the anterior face of the lens becomes more convex or flatter, as the case may be. This observation affords the proof that accommodation is due to the varying convexity of the anterior surface of the lens. Fishes are normally short-sighted, and accommodation for a distant object is effected with them by moving the lens towards the retina.

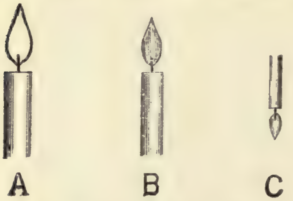

FIG. 163.—DIAGRAM OF THE KATOPTRIC TEST.

A, From the anterior surface of the cornea; B, from the anterior face of the lens; and C, from the posterior face of the lens.

The ciliary muscle is governed by the short ciliary nerves derived from the ciliary ganglion, and, therefore, indirectly from the third cranial nerve. In the human subject the constrictor fibres of the iris and the ciliary muscle are paralysed by atropine, but in the cat (as first pointed out by Lang and Barrett*), the dog, and certainly in the horse, there is no evidence that any paralysis of the ciliary muscle takes place under atropine, though the pupil dilates. Under the full effect of atropine all these animals can see objects quite close to the eye, and this they could not do if the ciliary muscle were paralysed.

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* 'The Refractive Character of the Eyes of Mammalia,' *Royal London Ophthalmic Hospital Reports*, vol. xi., part ii.

Defects of the Eye.—Eyes which possess the power of seeing objects distinctly a few inches from the eye to infinity are known as **Emmetropic** (Fig. 164—1); but all eyes do not possess this range of vision, owing to their shape, or, more correctly, to the length of the eyeball. **Myopia**, or short sight, is due to the eyeball being too long, whereby the picture is formed in front of the retina, and only a confused and blurred image falls on it (Fig. 164—3). The writer's observations show that the majority of horses are slightly short-sighted.* **Hypermetropia**, or long sight, is due to the eyeball being too short, whereby, though vision may be perfect for distant objects, those near at hand are not distinctly seen, the picture being brought to a focus behind the retina (Fig. 164—2). It is obvious that a concave glass which scatters rays is the remedy for myopia, while a convex lens which converges them is the appropriate glass for hypermetropia.

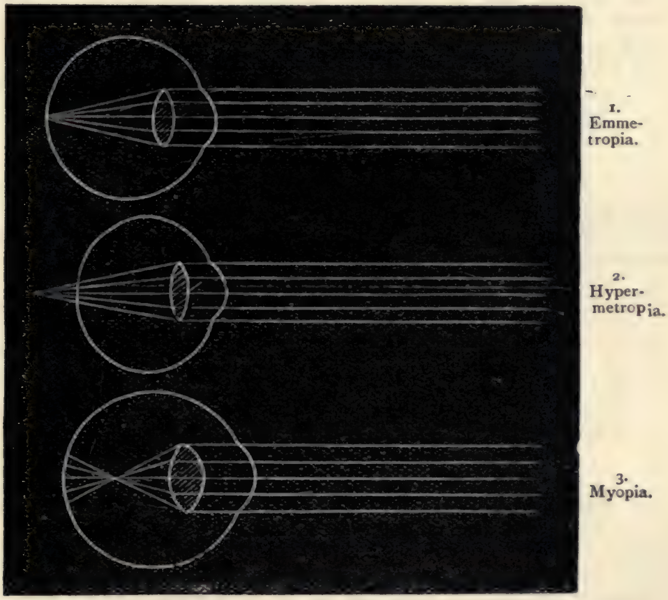

FIG. 164.—DIAGRAM OF AN EMMETROPIC, HYPERMETROPIC, AND MYOPIC EYE, TO ILLUSTRATE WHERE THE FOCAL POINT EXISTS (KIRKE).
In 2 the short eyeball causes the focus to form behind the retina; in 3 the long eyeball causes the rays to come to a focus in front of the retina.

Astigmatism is a defect due to irregularities in the curvature of the cornea or lens, generally the former. The result of this condition is that the rays of light passing through one meridian of the eye are brought to a focus earlier or later than those passing through the meridian at right angles to it. The horse is very commonly astigmatic ; the horizontal is generally the meridian of least curvature, and corresponds to the long diameter of the pupil.

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* 'The Refractive Character of the Eyes of Horses,' Proceedings of the Royal Society, No. 334. 1894.

Errors of Refraction.—The amount of error of refraction is small in animals, but it is somewhat remarkable that the nature of the error should have proved so variable in the hands of different observers, and it has been suggested that myopia in horses is more frequent in the northern countries of Europe.

In fifty-four horses the writer found, of 100 eyes examined :

1 per cent. emmetropic.
3 per cent. hypermetropic.
90 per cent. myopic.
6 per cent. mixed astigmatism.

All other observers have found a larger amount of hypermetropics, a smaller proportion of myopics, and a much larger proportion of emmetropics.* For example :

	Emmetropic.	Hypermetropic.	Myopic.
	Per Cent.	Per Cent.	Per Cent.
Del Seppia (Italy) -	22	53	13
Möller (Germany) -	34	22	44
Noli - - - -	17·5	69	13

As stated above, the amount of error existing is small, the chief visual defect, exclusive of myopia, being astigmatism ; the number of astigmatic horses is remarkable, about 50 per cent. Low degrees of astigmatism are of no importance, but a markedly astigmatic eye may account for the frequency of 'shying.' According to the observation of Long and Barrett, the cow appears to be hypermetropic, and the eye suffers from astigmatism. In dogs and cats they found the refraction to approach emmetropia closely, but in nearly all the wild animals examined by these observers the refraction was hypermetropic. Recent work on the eye of the dog shows it to be always myopic.†

Berlin, whose work with Eversbusch on the eyes of animals is a classic, says the horse is slightly hypermetropic, but not sufficiently to prevent the eye being called emmetropic.‡

The **Movements of the Eyeball** are brought about by means of the ocular muscles ; in this way the globe of the eye can be rapidly turned in any direction. The movements are somewhat complex, for in some of the lower animals—for example, the horse—the eyes are laterally placed in the head, so that vision is commonly single-eyed, and not binocular, as in man. The eye that is viewing an object situated to one side and moving to and fro is being followed in this muscular movement by the eye which does not see; but this does not apply to all animals, as shown by Harris. The movements in the horse are conjugate, but this only occurs so long as monocular vision is practised. If both eyes be directed to an object situated to the front binocular vision becomes possible, and now the movements are no longer conjugate, but opposite, for while the left eye is inclined to the right, the right eye is inclined to the left. Another complication in the ocular muscles is due to the movement of the head; it was first pointed out by Lang and Barrett that in the rabbit and guinea-pig, no matter what position the head occupied, the pupil was always kept vertical. If the head of the horse or ox be raised or depressed to the fullest possible extent, the muzzle being at one time on the ground, at the next high in the air, it will be

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* *Il nuovo Ercolani*, 1909.

† R. Boden, *Archiv für Vergl. Ophthalmologie*, January, 1910.

‡ At the time Berlin wrote, the method of determining the refraction errors of the eye by 'skiascopy' was hardly known.

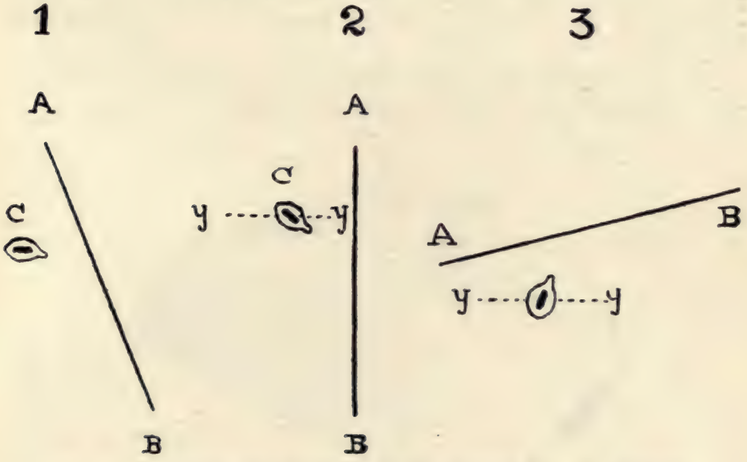

FIG. 165.—DIAGRAM TO ILLUSTRATE THE ROTATION OF AN EYEBALL.

A, B, Middle line of the face; C, the eye.

In 1 the head is supposed to be in the ordinary upright position and the pupil horizontal.

In 2 the head is depressed as in grazing; if the direction of the pupil remained unaltered, it would be as represented—viz., oblique. It is, however, horizontal, as indicated by the dotted line *y y*.

In 3 the head is elevated. If the direction of the pupil in 1 had undergone no change, it would now be nearly vertical, as shown, but the torsion of the globe maintains its horizontal direction *y y*.

found that the eyeballs rotate like a wheel, so that the pupil is still kept horizontal; if it were not for this the pupil in the uplifted head would be vertical and in the depressed head oblique (Fig. 165). When the head is elevated the eyeball becomes depressed to such an extent that the sclerotic shows largely above, while the cornea partly disappears beneath the lower eyelid. When the head is depressed to the ground, no more sclerotic shows than when it is in the ordinary position; the probable cause of this will be mentioned presently. The horizontal pupil behaves like a spirit-level, and maintains the animal's position to the outside world by keeping the eyeball always horizontal.

The **Muscles of the Eyeball** (Fig. 166) are seven in number—viz., four *recti*, two *oblique*, and one *retractor*. The use of the recti is clear enough: they rotate the eye in four directions—outwards, inwards, upwards, and downwards. The two oblique muscles rotate the eye in opposite directions around its antero-posterior axis. When the superior oblique contracts, it pulls the temporal side of the eyeball upwards, and if it were not counteracted by the inferior oblique it would continue to contract until the pupil became vertical like that of the cat; the inferior oblique pulls the temporal side of the eyeball downwards—in other words, these oblique muscles produce a torsion of the globe or swivel rotation, and their action is regulated from the semicircular canals of the internal ear (see p. 484). The retractor partly withdraws the eye in its socket.

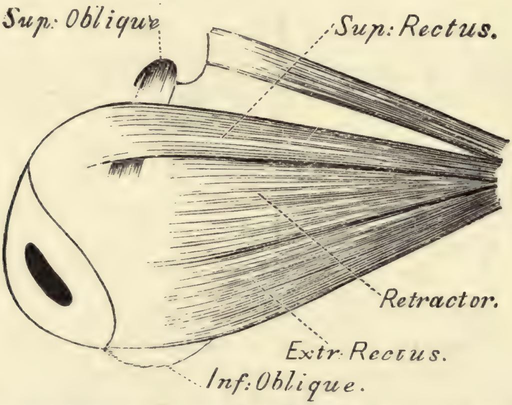

FIG. 166.—THE MUSCLES OF THE LEFT EYEBALL OF THE HORSE VIEWED FROM THE TEMPORAL SIDE.

The nerves supplying the muscles of the eyeball with motor power are the third pair to all excepting the external rectus and superior oblique, the external rectus being supplied by the sixth pair, or abducens, and the superior oblique by the fourth pair, or pathetic ; so that three pairs of cranial nerves supply seven ocular muscles.

The chief movements of the eyeballs are backwards and forwards, corresponding to the directions described as outwards and inwards in man. During these movements it is evident that the external rectus of one eye is acting in conjunction with the internal rectus of its fellow, and such is always the case in monocular vision. Animals with the eyes not too laterally placed have, however, the power of monocular and also of binocular vision, but the latter is only produced by an internal squint, and the movements of the muscles are now no longer conjugate, for both internal recti are acting together (Fig. 167). Sometimes, then, the group of muscles employed in moving the eyeballs is the same in each eye, at other times it is not. The torsion produced by the superior and inferior oblique muscles is of value in the binocular vision of animals and in the vertical movements of the head. When the muzzle is raised, as previously described, the superior oblique muscle rotates the eyeball in its socket until the pupil is horizontal. The explanation of the cornea partly disappearing under the lower lid, and the sclerotic showing extensively above, appears to be due to a conjugate action of the inferior rectus muscle whenever the superior oblique is so employed. The inferior oblique is mainly employed with the internal rectus in pulling the eyes inwards for binocular vision ; also, as mentioned above, for maintaining the horizontal pupil when the head is depressed or raised.

Monocular and Binocular Vision.—The question of whether an animal is able to see a single object with both eyes depends entirely on the position of the eyes in the head. Eyes laterally placed, as, for example, in fishes, the hare or guinea-pig, are incapable of looking forward, owing to the anatomical arrangement of the parts lying between the two eyes. A laterally-placed eye possesses only panoramic vision ; two eyes, each possessing only monocular vision, command a very wide visual field. Eyes placed towards the centre of the face in which the visual axes are practically parallel, as in the case of man, monkey, cat, etc., enjoy binocular vision, which, though it loses in range, gains in quality, for in such eyes the perception of relief exists ; whereas eyes laterally placed, though enjoying keen sight, can only furnish relief and depth of objects in an imperfect manner. Between these two extremes of monocular and binocular visions is a third class, in which the vision, though mainly monocular, may also be binocular, and of these the horse furnishes an example. When dealing with the arrangement of the fibres in the optic nerve, it was pointed out that in some animals the decussation was complete—viz., all the fibres, say, from the right eye, passed to the left brain ; this is what exists for all eyes so laterally placed in the head that only monocular vision is possible.

In other cases a large proportion of the fibres do not cross in the chiasma, so that if these are proceeding from the right eye, they pass to the right brain. This condition exists in man and those animals with the eyes centrally placed in which binocular stereoscopic vision only exists. Between these comes another group, where a certain, but small, proportion of the fibres are direct, but the bulk decussate; and such we saw was the condition in the horse, in which it is stated one-sixth of the fibres only are direct. In man vision is binocular and stereoscopic, and the conditions for stereoscopic vision are that the visual impressions from the left halves of the two retinæ shall be superimposed on the left occipital cortex, while those from the right halves are similarly impressed on the right visuo-sensory area. An animal may have binocular vision; it is met with in some birds and reptiles, but, nevertheless, it is not stereoscopic, for the reason that there are no direct fibres in the optic nerve. In the cat and tiger there is, as in man, true stereoscopic vision, the visual axes being roughly parallel, and a sufficient number of direct fibres passing from the retina to the same side of the brain. Harris* considers that the presence of binocular or monocular vision in animals depends upon their feeding habits. Carnivora, in order to be quick and sure, have their eyes set well forward; in the herbivora, whose food does not run away from them, the eyes are laterally placed. In carnivorous birds, such as the owl, the presence of binocular vision (not stereoscopic) assists the accuracy of sight in twilight. Mott† regards the production of binocular stereoscopic vision as depending on the specialisation of the fore-limbs for prehension of prey; this would be less effective in the absence of stereoscopic vision, and he regards it as the determining factor rather than the nocturnal habits of animals.

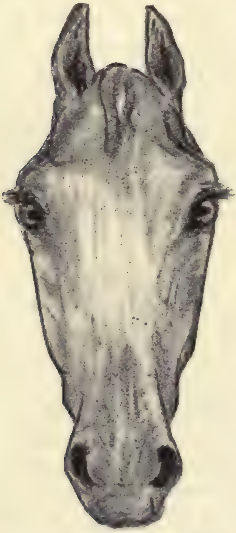

FIG. 167.—THE POSITION OF THE HEAD AND EYES IN BINOCULAR VISION.

When a horse directs both eyes to the front (Fig. 167) he produces a well-marked double internal squint, and is then capable of binocular vision. The eyes are rotated inwards and slightly upwards by the combined action of the inferior oblique and internal rectus; the pupils are not perfectly horizontal, but nearly so, and the pupillary opening is brought so far to the front that the inner segment of the cornea and iris entirely disappears beneath the inner canthus. In no other position than this has the horse binocular and presumably stereoscopic vision. Animals with their eyes situated on the lateral side of the head are capable of exercising monocular vision for all objects placed to one side of them, and even behind them. There is good vision out of the 'tail' of the eye and limited vision out of the tail of both eyes simultaneously employed (Fig. 168). When the attention of a horse is drawn to a distant object, either through interest or alarm, it is viewed with *both* eyes, the head being held very high, inclining to the horizontal, the ears 'pricked' and turned to the front. In this position it is evident the most sensitive area of the retina is exposed, and it is assumed that, like the *fovea* in man, the retina at this part is thinned out, and only cones exist. A horse can see an object on the ground immediately under his nose, and is able to see when grazing; this is because his face narrows below the eyes. When looking at a near object on the ground, he prefers to get his head low down in order to see it, and views it with *one* eye, the head being slightly twisted. Ordinary equine vision is monocular, yet the right eye blinks when an attempt is made to strike the left, though it cannot possibly see what is going on; and in the same way the right pupil contracts when the left is exposed to sunlight, though not to the same degree.

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* *Op. cit.*, p. 535

† *Op. cit.*, p. 541.

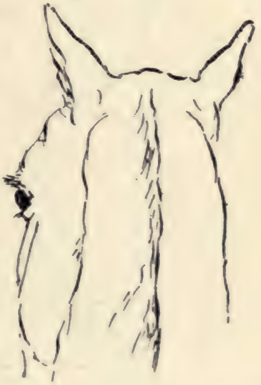

FIG. 168.—DIAGRAM ILLUSTRATING THE EXTENT TO WHICH A HORSE CAN SEE BEHIND HIM.

With the head straight to the front he can see out of the 'tail' of both eyes. By the least inclination of the head, as in Fig. 168, a large visual field behind him may be covered.

In man binocular vision is perfect, and the explanation afforded is that any part of one retina corresponds to the same part of its fellow; so that if the retinas be laid over one another, the left portion of one will lie exactly over the left portion of the other, and their upper and lower parts will equally correspond; but the temporal side of one eye does not correspond to the temporal side of its fellow, but to the nasal side. In Fig. 169 the two circles represent the two retinas divided into quadrants, L being the left and R the right eye; *a* and *c* in the left eye correspond to *a′ c′* in the right eye, and *b* and *d* in the left correspond to *b′* and *d′* in the right eye; but the optic nerve *o* is in the left segment of one eye, and the right segment of the other. When the two images of an object fall on corresponding points of the retinæ of man, vision is binocular, and only one object is seen; thus, if the rays fall on the right side of one retina, they must fall on the right side of its fellow. This is shown in Fig. 169: *vl* from X to X′ and X to X, are the two visual axes; if the object Y X Z be looked at, Z in each case falls to the left of the visual axis, and Y to the right—viz., on corresponding points—by which means, provided direct fibres exist in the optic nerves, so as to allow the impressions from the two right halves of the retinæ to pass to the right, and from the two left halves to pass to the left brain, the object is seen singly, with good perception of depth and solidity, but with loss of range. No matter how greatly the eyes of herbivora may be converged in order to see an object, the rays of light do not fall on the same side of the retina, but on *opposite sides* of it ; the diagram (Fig. 170) will make this point clear. The outer part or temporal side of the retina in the horse corresponds with the temporal side of the opposite eye ; while the nasal side cannot correspond with the nasal side of its fellow, as it is not possible for a ray of light from an object to strike both nasal sides at one time.

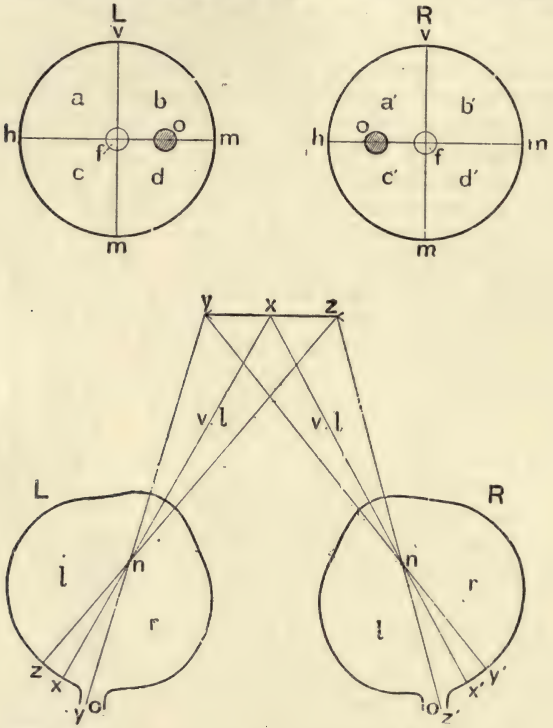

FIG. 169.—DIAGRAM ILLUSTRATING CORRESPONDING POINTS IN THE HUMAN EYE (FOSTER).

z' x' y' are points in the right eye corresponding to z x y in the left eye ; v. l. visual axis. The two figures above illustrate the corresponding points on the retina described in the text.

Mott points out that the conjugate movement of head and eyes in following a moving object assists the judgment in forming an idea of the rate of movement. In animals with panoramic or semi-panoramic vision, the visual range is increased by movements of the head rather than the eye. Steiner, quoted by Mott, showed that in the young animal the motor cortex of the cerebrum responds to excitation before the visual cortex; in the rabbit the motor is excitable on the ninth or tenth day, the visual not until the fourteenth, and not until the fifteenth day does the animal attempt flight if pursued. The dog is later; the eyes are opened on the fourteenth day, but it is not until the thirty-fourth that a dog avoids obstacles. He can see directly to his front, but an object projected laterally on the visual field is not looked for by head and eye movements. Mott points out that visual images alone do not convey to the mind the reality of the external world, unless associated with locomotion and previous tactile and kinæsthetic impressions, which appear necessary factors before visual impression can be translated and their meaning known. How true this is will occur to all connected with the care and management

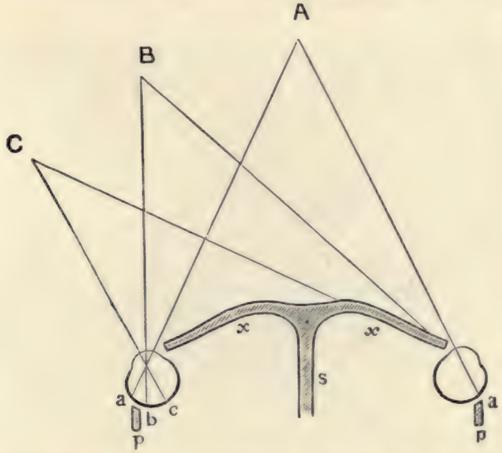

FIG. 170.—DIAGRAM SHOWING HORIZONTAL SECTION OF THE HEAD PASSING THROUGH BOTH EYEBALLS, TO ILLUSTRATE CORRESPONDING POINTS IN THE RETINA OF THE HORSE.

x, x, The frontal bones; *p p*, portion of malar bone entering into the formation of the outer rim of the orbit; *s*, the nasal septum. Rays of light proceeding from A are seen by both eyes, being imprinted on the temporal side of each retina at *a*; rays from B are seen at *b* in the left eye, but are not seen with the right eye; in the same way rays from C are imprinted at *c* in the left eye, but cannot be seen with the right eye.

of horses. The fear of an object may be immediately or shortly dispelled by allowing the animal to smell and examine it. The carelessness shown by some horses in jumping is corrected by a sharp rap on the shins, and future judgment assisted by a fall.

Cartilago Nictitans.—The retractor muscle of the eye withdraws the eyeball within the orbit, and the pressure thus produced within the cavity forces the *cartilago nictitans* forward, so that it may be made to sweep nearly the whole corneal surface. The reason why the cartilage is pressed forwards is due to the fact that, though naturally curved, it becomes flattened and straightened out by the pressure caused by retraction, and this shoots it forward ; when the pressure is removed, it retires through its own elasticity, and becomes curved once more. On the cartilage of some animals, especially the ox, is a small gland, termed the Harderian ; its use is to prepare an unctuous secretion, probably of a protective nature. Numerous glands, the Meibomian, are also found in the eyelids, which furnish an oily secretion, and prevent the overflow of tears.

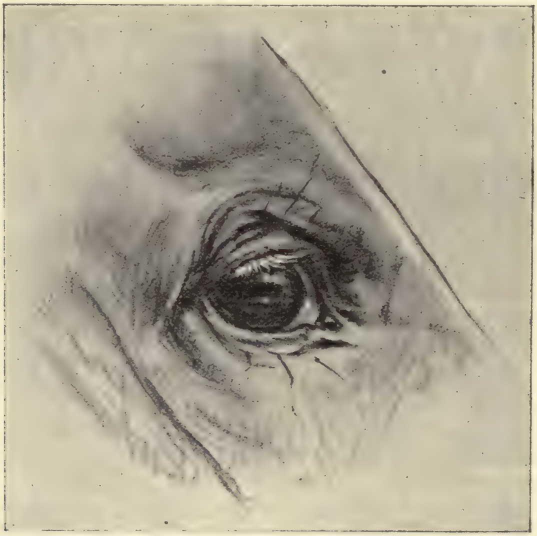

FIG. 171.—THE EYE OF THE HORSE.

The **Tears** are secreted by the lachrymal gland, which is placed on the upper surface of the eyeball ; they find their way into the conjunctival sac by numerous small tubes. The tears pass through the narrow *punctum* into the lachrymal duct, and so into the nostril; but it is essential that the punctum should be in contact with the globe, or else the tears run over the side of the face. The use of the tears is to keep the conjunctiva moist and polished, and to wash away foreign bodies.

The **Eyelashes** of the horse are peculiar. Those on the lower lid are very few and fine, whilst on the upper lid they are abundant, and exist not as a single but as a double row; the rows cross each other like a trellis-work, but without interlacing; these eyelashes are very long and strong (Fig. 171). A few protective hairs grow from the brow and below the lower eyelid; in some horses they are 4 or 5 inches in length. They appear to be in connection with nerve terminations, and their delicacy to the sense of touch is remarkable. The function of these hairs is protective; they give the eyes warning of danger.

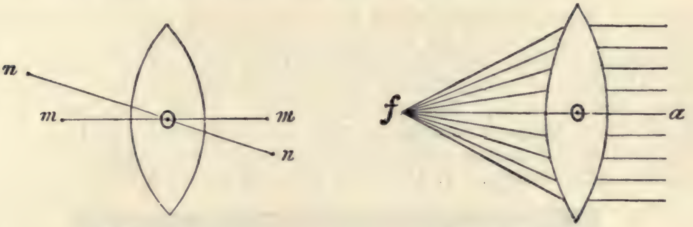

Fig. 172. Fig. 173.

Figures illustrating the Action of Lenses upon Rays of Light passing through them.

Fig. 172—biconvex lens: O, optical centre; *mm*, chief or principal axis; *nn*, secondary axis.

Physiological Optics—*Passage of Light through Lenses.*—All rays of light are diverging, but so slight is the divergence of the rays from distant objects, that for the purposes of the eye they are practically regarded as parallel. All rays proceeding from an object situated at from 6 metres (20 feet) to infinity from the front of the eye are considered as *parallel rays;* all rays within 20 feet from the cornea are *diverging rays.* Obviously the nearer the object to the cornea the greater the divergence, so that there is more divergence in the rays proceeding from a body 1 foot from the eye than in one 10 feet from the eye; conversely, the farther the object is from the eye the less divergent the rays until that point is reached beyond 20 feet at which the rays may be regarded as parallel.

A convex lens has two curved surfaces, and a line drawn through the centre of these two surfaces is known as the *principal axis* of the lens (Fig. 172, *mm*). The essential idea of a double convex lens is that it is thicker at the centre than at the edges. Situated on the principal axis of a biconvex lens at a point in its interior is the *optical centre* (Fig. 173, O); any other straight line passing through the optical centre is termed a *secondary axis* (Fig. 172, *nn*).

When *parallel* rays of light (Fig. 173, *a*) pass through a convex lens they are refracted and brought to a point *f* on the opposite side of the lens, known as the principal focus; the only rays not refracted are those passing through the centre of the lens—viz., those coinciding with the principal or secondary axes. The converse of this is also true—viz., *divergent* rays proceeding from the principal focus of a lens *f* pass through and are rendered parallel (Fig. 173).

The distance from O, the optical centre of the lens, to *f*, its principal focus, is known as the focal length of the lens. If the divergent rays, instead of proceeding from the focus of the lens, proceed from a point *l beyond the focus*, then the rays, on passing through the lens, are not rendered parallel but *convergent* (as the refractive power is more than sufficient to render them parallel), and they come to a focus again on the other side of the lens at the point *v*. The distance from the lens at which they come to a focus depends upon the distance of the luminous point from the lens on the opposite side; thus the nearer the luminous point *l* to the principal focus *f*, the farther will the focus on the opposite side recede, and *vice versa*. The two foci *l* and *v* are termed *conjugate foci*, and they bear a definite relationship. If the rays of light proceed from a point L (Fig. 175), which is nearer to the lens than the principal focus F, the lens is unable to refract the rays sufficiently, and they issue from the opposite side divergent (Fig. 175, *dd*).

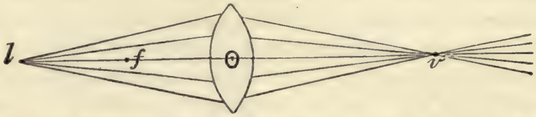

FIG. 174.—Rays of light passing through a convex lens from *l* at a point beyond the focus *f*, cross at some point *v*, and invert the image.

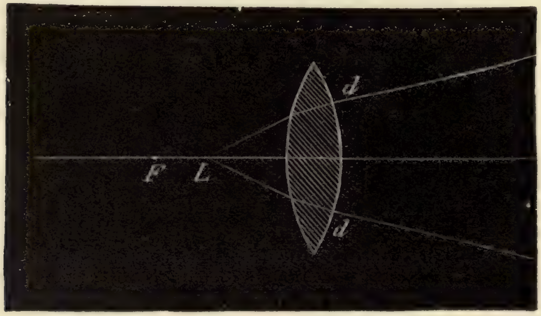

FIG. 175.—Rays of light from a point L, between the focus F and the lens, diverge when passing through a convex lens.

Parallel rays of light passing through a *concave* lens, instead of being refracted to a focus, are bent and become divergent, so that a concave lens has no real focus; but if the divergent rays be produced backwards so as to meet on the principal axis of the lens, the point where they meet is called the *negative focus* of the lens.

Spherical Aberration.—The rays of light passing through a convex lens are not all equally refracted, those passing through the circumference being more bent than those passing near the centre; the result is that the rays do not all meet in the same point, those passing through the circumference of the lens coming to a focus earlier than those passing near the centre. This defect, known as 'spherical aberration,' is remedied in the eye by the introduction of a diaphragm or iris, which prevents some of the rays of light from passing through the circumference of the lens; spherical aberration is further prevented by the fact that the refractive index of the central part of the lens is greater than that of the circumference. Spherical aberration produces indistinctness of vision by the production of circles of diffusion, caused by those rays which meet too early crossing each other and forming a circle.

Chromatic Aberration is due to the decomposition of white light into its primary colours by passing through a prism or a convex lens—viz., a spectrum is formed. The colours of the spectrum are differently refracted, the red being the least bent, the violet the most; when, therefore, the red is distinctly seen, the eye is not focussed for the violet. There is no compensation in the eye for chromatic aberration. The defect is usually not noticeable, because it is small in amount, and is rapidly corrected by alterations in accommodation.

Schematic and Reduced Eye.—When a ray of light enters the eye, it has to pass through four surfaces, and, including the air, four media. There are two surfaces to the cornea, anterior and posterior, and two surfaces to the lens, anterior and posterior; each of these surfaces differs in curvature. As media, there are the aqueous and vitreous humours and the crystalline lens; the latter is further complicated by not being of the same refractive index throughout. The formation of an image in such a complex optical system would be difficult to understand, were it not possible to construct theoretically from it a simplified eye, or, as it is known, *a schematic* eye. The basis of its construction is, that so long as a complex system has its surfaces and media 'centred'—that is, symmetrically disposed around the optical axis—it is possible to deal with it as if it consisted of two surfaces and two media—viz., the *schematic* eye—and even to simplify it still further to one surface and two media, the *reduced* eye, the media in the latter being air and water. In such a simple optical system it is readily possible to trace the paths taken by the rays of light, and so understand the formation of an image on the retina of the eye.

Cardinal Points.—The most simple optical system which can be devised has an *optic axis* (OA, Fig. 176)—viz., a line passing through its centre perpendicular to its refractive surface (*apb*). On the optic axis is situated the centre of curvature of the refracting surface; this centre is known as the *nodal point n*. All rays of light which strike the refractive surface perpendicularly, such as O, *m*, pass through the nodal point and are not refracted; all rays of light *parallel* to the optic axis, such as *cd*, strike the refractive surface obliquely and are refracted, and the point where they meet is called the *principal posterior focus*, F_2. On the optic axis, in front of the refractive surface, is situated a point F_1 known as the *principal anterior focus*; rays proceeding from this point strike the surface obliquely, and are so refracted as to be rendered parallel (*ef*) to the optic axis (OA). To these must be added the *principal point p*, that is, the point where the refracting surface cuts the optic axis. These various points are known as the *cardinal points* of the simple optical system we have imagined. For a more complex system such as the eye, even when simplified, there are two nodal points, two principal foci, and two principal points; but with the reduced eye, where there is but one surface and two media, the two nodal points become one, and the two principal points one.

Dioptrics.—In order to be able to calculate the position of the cardinal points of the eye, certain data must be known, such as the refractive index of the media, the radius of curvature of each refracting surface, the distance from the cornea to the lens, and the thickness of the latter. A very slight error in the determination of these may produce a considerable error in calculation, so that all measurements made by us on the frozen eyes of horses are rejected as wanting in accuracy; but as an illustration of the measurements of the actual and reduced eye, those furnished by Berlin* are here given. This measurement shows the eye to be long-sighted, the retina being in front of the second principal focus. It will be remembered (p. 546) that, according to the writer's observations, the majority of horses are slightly short-sighted, in which case the point F_{II} will fall in front of the retina.

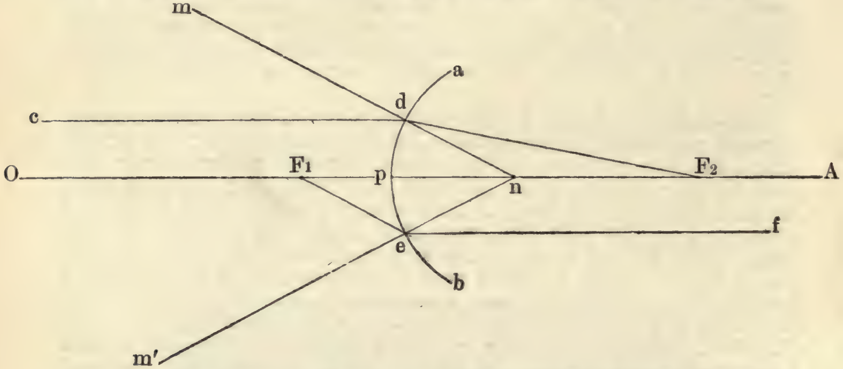

FIG. 176.—THE CARDINAL POINTS OF A SIMPLE OPTICAL SYSTEM (FOSTER).

OA, Optic axis; *apb*, a curved spherical surface; *n*, nodal point; F_2, principal posterior focus; F_1, principal anterior focus; *ef*, rays proceeding from F_1, rendered parallel to the optic axis; *p*, the principal point; the rays *md*, O*p*, and *m'e*, pass through the nodal point *n* and undergo no refraction; the rays *cd*, parallel to the optic axis, are refracted, and meet at F_2.

The *simplified* or *reduced* eye (Fig. 178), consisting of one surface and two media, gives for the horse, according to Berlin, the following values:

F_I the first principal focus, is situated 27 mm. in front of the cornea.

F_{II} the second principal focus, is situated 36 mm. behind the cornea.

K to *a*, the distance from the nodal point to the retina, 25·5 mm.

H to *a*, the distance from cornea to retina, 34·5 mm.

Formation of a Retinal Image.—Rays of light falling on the eye, as from the arrow XOY (Fig. 179), issue as a pencil of rays from every point of the arrow; the pencil containing the central ray is known as the principal ray. All principal rays *aa'* pass

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* *Zeitschrift für Vergleichende Augenheilkunde*, Heft 1, 1882.

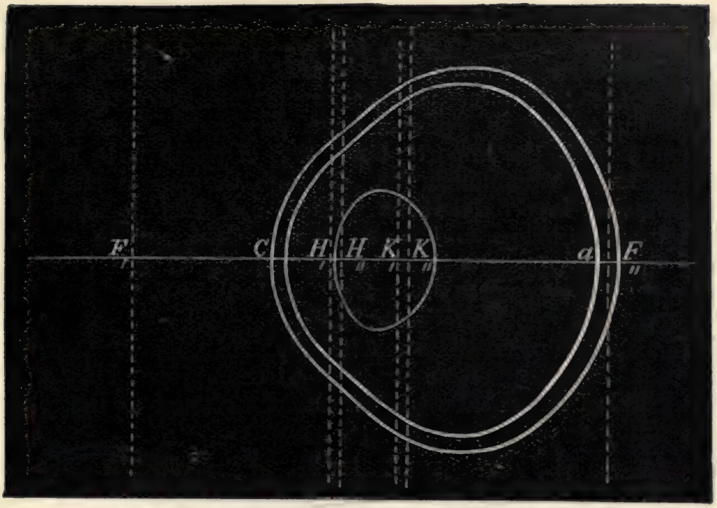

FIG. 177.—THE CARDINAL POINTS OF THE EYE OF THE HORSE (BERLIN).

$F_{,}$ is the first principal focus, situate 18·38 mm. in front of the cornea.
C is the anterior principal point.
$H_{,}$ is the first principal point, distant from the cornea 8·13 mm.
$H_{,,}$ is the second principal point „ „ „ 9·28 mm.
$K_{,}$ is the first nodal point „ „ „ 17·03 mm.
$K_{,,}$ is the second nodal point „ „ „ 18·18 mm.
$K_{,,}$ to *a* is the distance of the retina from the second nodal point, 25·32 mm.
C to $F_{,,}$ is the distance from the cornea to the second principal focus (which Berlin shows to be behind the retina), 44·69 mm.

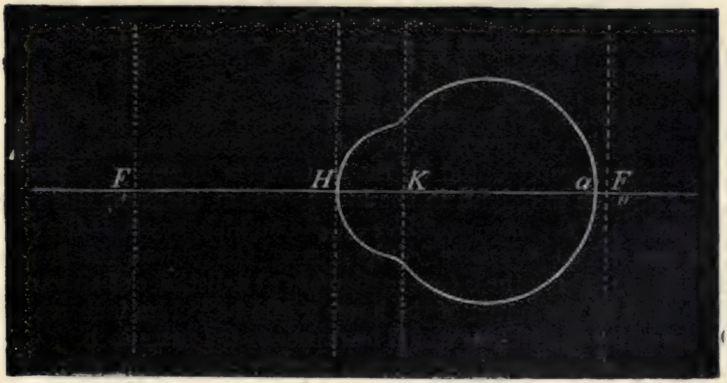

FIG. 178.—THE CARDINAL POINTS OF THE REDUCED EYE OF THE HORSE (BERLIN).

through the nodal point *n* without undergoing refraction, while the rays *bc* and *b′c′* are refracted to a greater or less extent, so that in this way the retinal image becomes inverted, and very much smaller than the object it represents ; it is a miniature though perfect representation of the object presented to the eye. The chief refraction undergone is at the anterior surface of the cornea ; doubtless the other media also refract, the lens, for example, but an eye can have very good distant vision without a lens, the important function of which is to provide the means for accommodation. Though the retinal picture is so completely inverted that the right hand of the object becomes the left of the image, and the top becomes the bottom, yet the mind does not perceive the image as inverted, but mentally refers the picture, not to the retina, but back to the object. In Fig. 179, the angle XnY is equal to the angle Y*n*X. The angle X*n*Y is spoken of as the *Visual Angle*, and all objects having the same visual angle form the same sized picture on the retina. By the aid of the visual angle the size of an image on the retina may be calculated, provided the distance of the nodal point from the retina is known. Thus at the distance of a mile, a man 6 feet high is represented on the retina of a horse by an image $\frac{1}{880}$ of an inch in height, in the human eye at the same distance the picture of the man would be $\frac{1}{1500}$ of an inch, or about the size of a red blood-corpuscle. The nearer the object the larger the image ; taking the 6-foot man again at a distance of 10 yards, his height on the retina of the horse would be $\frac{1}{5}$ of an inch, whilst on the retina of a man it would be rather over $\frac{1}{8}$ of an inch.

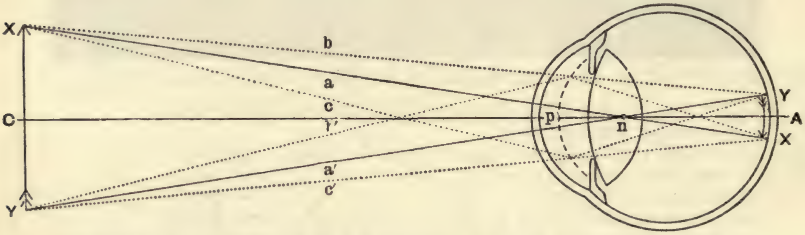

FIG. 179.—DIAGRAM OF THE FORMATION OF A RETINAL IMAGE (FOSTER).

a, Principal ray of the pencil of light proceeding from X ; *a′*, principal ray of the pencil of light proceeding from Y ; the principal rays pass through the nodal point *n* without being refracted ; the other rays, *bc* and *b′c′*, are refracted. In this way the arrow XY forms a smaller inverted image of an arrow on the retina YX.

Theory of Vision.—The change that enables the vibratory ether to start a nerve impulse by its action on the retina is unknown. Cutting or stimulating the optic nerve causes no pain, but produces a flash of light ; it is only when the physiological stimulus occurs through the retina that an object is seen. It is known that electrical changes occur in the eyes, associated not only with flashes of light, but to what has been termed 'flashes of darkness.' If an excised eye be suitably connected to a galvanometer, the eye being kept in the dark, an electrical change occurs when light is transmitted through the pupil, and there is a similar electrical change when the light is withdrawn. The sensitiveness of the eye to these reactions increases by its being kept in the dark. Not all ether-waves are capable of being perceived. The eye, excellent as it is, is not free from optical defects, as we have seen at p. 545. Similarly, the retina is not sensitive for those red or violet rays known as *ultra*, though the photographic plate is capable of recording them.

A photo-chemical theory of vision, based on the ready decomposition of **visual purple**, has been proposed. The visual purple is limited to the external segments of the rods, the cones contain none; under the influence of light the pigment is bleached, and in this way a retinal photograph, or *optogram*, may be obtained in the eye of the frog or rabbit which has been suitably prepared by being kept in the dark. If the pigment be extracted and brought into solution, as it may through the action on it of bile-salts, the coloured solution thus obtained is bleached on exposure to light. There is good reason for thinking that some such change occurs in the living eye. It is known that the restoration of colour to the rods is effected by contact with the pigment of the choroid. Nevertheless, this pigment is not necessary to vision, as in the eyes of some animals it is absent, notably in the hen and pigeon; further, it is absent from the area of acute vision in man—viz., the fovea.

An eye adapted to light and an eye adapted to darkness is a sensation with which all are familiar on passing from a light to a dark room; the vision improves by waiting in the dark, and it can be shown in man that the improvement does not occur over the cone area—viz., the fovea—but over the peripheral field, where the rods predominate. The explanation of the vision of night-seeing birds and animals probably lies in this function of the purple-coated rods; while acute daylight vision is probably the essential function of the non-pigmented cones. Neither the hen nor the pigeon, whose habits are diurnal, can be regarded as possessed of eyes defective in acuteness of vision, yet neither possess visual purple. On the other hand, neither possess vision suitable for night-time. In the bat visual purple has been found; in the owl it exists in abundance. It seems justifiable to believe that the difference between eyes suited for daylight and darkness largely hinges on the question of visual purple, by which the irritability of the rods is increased in dim light, and vision is facilitated in illuminations of low intensity. Too little is known of the *tapetum lucidum* to enable its function in connection with night vision to be determined ; it is fair to suppose that it enables an animal to see better in a dim light, though, as stated at p. 537, it cannot enable it to see in the dark.

Pathological.

Diseases of the eye in the lower animals are not numerous, and are only of great importance in those required for work, particularly work of a special kind requiring acute vision, and in horses used for riding purposes. A horse with defective vision may do good service in draught, but with a riding horse it may prove a serious matter. **Injuries** to the eyes of horses are frequent—lacerated eyelids from projecting nails and hooks in the stable ; injuries to the cornea and punctures of the eyeball caused in the hunting-field, and more commonly in the stable. The animal can offer no protection to its eyes other than by the use of the retractor muscle. As might be expected, the most serious injuries to the globe of the eye are produced by the smallest objects. A blow on the eye from a large object may not leave a mark on the eyeball, while a blow from a stick or the end of a lash may destroy vision. **Errors of accommodation** have been discussed on p. 545, and need not be dealt with further ; correcting lenses have been employed, but are never likely to prove popular. **Shying** is not necessarily due to defective vision, though there can be no doubt that both astigmatism and short sight are responsible for many cases. The most destructive eye disease is the so-called **Specific Ophthalmia**, an attack of which affects almost every tissue in the globe of the eye. Something resembling it has been observed in cattle in South Africa, but, speaking broadly, there is no eye disease in other animals or man which for intensity and destructiveness can approach it. When horses were taken less care of than they are at the present day, and the laws of health were less understood, the disease was rampant throughout Europe. In this country it is now relatively rare, but is still common both on the Continent of Europe and in North America. It always leads to destruction of one or both eyes, extending over a series of attacks, each of which leaves the eye worse than before. **Cataract** is the most common internal disease of the eye in horses, and a serious cause of unsoundness. Unlike cataract in the human subject, the lens may not become entirely opaque—in fact, total opacity is the least frequent condition met with. Spots of opacity, one or more, sometimes no larger than the head of a pin, and generally situated in the line of vision, represent the bulk of cases of cataract. There are some forms of cataract which escape detection when the eye is merely illuminated from the front, and can only be seen when the lens is illuminated from the back by means of the ophthalmoscopic mirror. In fact, no one by the ordinary method of eye examination can, without risk of error, declare an eye free from cataract without using the mirror of the ophthalmoscope. There are many cataracts concealed by the margin of the pupillary opening which only become visible when the eye is examined with this instrument.

SECTION 2.

Smell.

The Olfactory Organ.—The nasal chambers are divided by a septum, and each chamber contains the turbinated bones. It has been observed that acuteness of smell is often associated with large and extremely convoluted turbinates. By the position of these bones the nasal passage may be divided into two channels, one which lies next the floor of the chamber, which, from its obvious communication leads directly to the respiratory passages, and another channel which lies above it and leads to structures situated very high in the face and nose. One is known as the respiratory and the other the olfactory passage. But apart from this there are differences in the physical characters of the mucous membrane of the nasal chambers ; that of the olfactory region differs from the respiratory portion in being thicker and of a yellowish tint, and it is in this membrane that the fibres of the olfactory nerve are distributed. Both the respiratory and olfactory portions of the nasal chambers are supplied with sensation by the fifth pair of nerves. In the horse the nasal chambers are of extreme importance, inasmuch as he is the only animal we are called upon to deal with which is unable to breathe through the mouth ; the majority of animals can breathe through both nose and mouth, but owing to the extreme length of the soft palate in the horse this is under ordinary circumstances impossible. So far as respiration is concerned the question of the nostrils has been dealt with (p. 115), but the arrangement of that portion devoted to the sense of smell has yet to be considered.

Olfactory Nervous Mechanism.—From the olfactory tracts in the brain the olfactory lobes are formed, which in some animals possess a well-marked cavity, in others only a canal. In the cavity some fluid is contained which communicates with the cerebro-spinal, and notably in the horse with that contained in the lateral ventricles. From the large olfactory bulbs non-medullated nerve fibres are given off, which penetrate the cribriform plate of the ethmoid, and ramify over the mucous membrane, covering the upper portion of the septum, the superior turbinated bone, and the upper third of the superior and middle meatus.

These nerve fibres terminate in olfactory sense organs, which are specialised nerve cells, from the free end of which project a tuft of hair-like processes, which are acted upon by olfactory stimuli. Tracing these nerves backwards into the brain, they are found to terminate in globular bodies in the olfactory lobes, where they connect with the special cells of this region through the dendrites of the latter. The axons from the new cells are continued into the olfactory tracts of the brain by means of bundles of fibres, some of which terminate in the tract; others cross to the opposite side, to end in the grey matter of the hippocampal lobes; others pass to the hippocampal lobes of the same side. The sense of smell is located in this region, but the connections of the olfactory tract are numerous and incompletely known. The olfactory area is interesting developmentally, as being the first part of the brain to put in an appearance, showing the extraordinary importance of the sense of smell in animals very low in the scale. In animals possessing acute sense of smell the olfactory regions are highly developed in others, like man, where additional protective instincts have subsequently appeared, the sense of smell is not so acute, and the central representation accordingly greatly reduced. In animals where the sense of smell is lost, as in the porpoise and most fishes, the olfactory region is absent, while in others, like the shark, which is guided entirely by this sense, its development is extraordinary. In a shark 25 feet long the olfactory nerves spread out over an area of 12 to 13 square feet (Halliburton).

The Olfactory Stimulus.—Before an odour can affect the olfactory nerves it has to diffuse into the higher cavities of the nasal chambers, and from being gaseous it must become dissolved in the fluid which bathes these surfaces, for a dry olfactory surface is insensible to smell. We have no idea of the nature of the particles which constitute an odour, but it is supposed that they act chemically on the hair cells. The odour of a body can be detected with greater accuracy by 'sniffing'; by this inspiratory act no time is lost in diffusion occurring between the respiratory and the olfactory region, as the odoriferous particles are forcibly drawn upwards. Colin performed a tracheotomy in horses, and tied the trachea above the incision. Under these conditions no air could pass up into the nasal chambers excepting by diffusion. Animals so treated were unable, with their eyes covered, to detect the presence of hay or oats. A stallion, however, under these conditions, was able to recognise a mare, though he failed to recognise food.

Olfactory Sensations.—There are certain odours which excite the olfactory organs more readily than others; thus flesh, blood, and offal have a remarkably stimulating effect on the carnivora, whilst grass, grain, and vegetable products generally, stimulate the herbivora. The odour of blood or flesh is evidently repulsive to the herbivora, and may even cause nervousness and fright;

there are exceptions to this, for horses have been known to eat meat with evident pleasure. The herbivora have a remarkably keen scent; antelopes and deer have the power of detecting the presence of an enemy a considerable distance away, and it is evident that in most animals the sense of smell plays a more important part in their daily lives than with ourselves.

The acute sense of smell in the herbivora is a protective mechanism. Their sight, comparatively speaking, is not acute, certainly nothing like so keen as that of the animals by whom they are hunted. Horses are quite conscious of the presence of a lion, and exhibit great alarm and anxiety when one is about. The sense of smell is also popularly believed to afford instruction to animals in distinguishing poisonous from non-poisonous plants, and the organ of Jacobson, which is well developed in the herbivora, was supposed by Cuvier to afford this protection. Smell, however, plays a very unimportant rôle in this connection. Cattle-poisoning as the result of grazing is common all over the world, and especially in South Africa. Experience is here the best master, and survivors may generally be left on a pasturage known to contain poisonous plants, for they have learnt to avoid them.

It is through the sense of smell that the male is attracted to the female during the 'œstrous' season, and not only can the odour of a female in this condition be detected at a considerable distance, but the smell is evidently most persistent. By the sense of smell animals have the power of recognising their own offspring; a cow which has lost her calf will yield milk for weeks to a 'dummy' clothed in the skin of the dead calf, and she can recognise the difference between her 'dummy' and that belonging to another cow. If the skin of a young animal, kid, for instance, be dressed with an agent which disguises the body-smell, the mother is unable to recognise her young. The odour of food is readily recognised by the herbivora, though to the human senses all the grains are equally free from any smell but that of the sack which contains them. Without tasting it, a horse will refuse a grain he is not familiar with. It is possible that everything and everybody has a distinctive odour—at least, it would appear to be so from the remarkable manner hounds will follow a scent, or a dog recognise his own master in the dark from amongst a crowd of other persons. In the case of hounds, the amount of odour required to stimulate the olfactory organ must be something too infinitesimal for expression.

The elevation of the upper lip in the horse is associated with the sense of smell. The stallion, on approaching a mare, exhibits this evidence of the pleasurable impression on his olfactory organs, but he does exactly the same after having had a draught of aloes poured down his throat, the bitterness of which he greatly resents.

The sense of smell rapidly becomes blunted—at any rate, in ourselves; any oppressive odour is always more marked when first detected. The writer has never satisfied himself that animals are conscious of an offensive odour. Garbage is evidently not offensive to a dog; horses certainly take no notice of the smell from putrefying bodies, though they refuse to pass them if visible, but that is only because they do not expect to see either men or horses in any other than an upright attitude.

SECTION 3.

Taste.

The sense of taste is largely, though not quite, dependent upon the sense of smell. There are certain substances which cannot be distinguished when the nose is closed, there are others which can be readily distinguished by the tongue alone. This has led to a **classification of taste** sensations of which four qualities exist—viz., *sweet*, *bitter*, *acid*, and *salt*. Animals are certainly capable of distinguishing all of these. It is probable that each distinct taste affects a particular part of the tongue ; in man it has been shown that the back part is sensitive to bitter tastes, the tip to sweet and saline tastes, the sides to acid tastes, while the middle portion of the tongue is insensitive to any taste. The *flavour* of a substance is not obtained by the sense of taste alone, but by the union of the senses of smell and taste. Without smell taste would be nearly impossible.

Tongue Papillæ.—The papillæ of the tongue are spoken of as *filiform*, *fungiform*, *circumvallate*, and *foliate*. The *filiform* occur over the upper surface of the organ, and in the ox impart to it its characteristic roughness. The *fungiform* papillæ exist principally on the lateral parts of the tongue ; the *vallate* are found far back on the dorsum, and are only two or three in number in the horse, twenty or thirty in the ox. The *foliate* papillæ are characteristically present in the horse, forming a large projection in front of the pillars of the soft palate. There are none in the ox, but they are very markedly present in the rabbit. The filiform are in function chiefly tactile, the fungiform, circumvallate, and foliate papillæ, are associated with the sense of taste, and in their structure are found the special nerve organs of taste, known as **taste buds,** bulbs, or taste goblets. These are balloon or barrel shaped bodies, the walls of which are formed of elongated cells resembling the staves of a barrel. This structure is open top and bottom ; the nerve fibrils enter below, while at the outer free end is the gustatory pore, or opening into the interior of the body of the bulb by which fluid finds its way in. The interior of the goblet or bulb is filled with two kinds of cell closely similar to those of the olfactory organ. Of these some are of a somewhat cylindrical shape, and are probably sustentacular. The others are rod-shaped, and have at their outer ends a hair-like process which projects at the pore. It appears to be essential to taste that fluid should readily find its way into the pore, and as a provision to ensure this the papillæ containing the buds are situated close to glands. M'Kendrick states that in a single circumvallate papilla of the ox 1,760 taste goblets have been counted. The goblet cells are not strictly limited to the tongue, but have been found in the palate, epiglottis, and even in the larynx.

Nerves of Taste.—It will be remembered (p. 519) that the posterior third of the tongue is provided with sensation by the glosso-pharyngeal nerve, the anterior two-thirds of the organ by the lingual branch of the fifth pair. These two nerves, besides endowing the tongue with sensation, are also concerned in carrying those impulses connected with the sense of taste. The cortical centre for taste is not definitely known, but is considered to lie close to that of the olfactory sense in the hippocampal lobe. It is believed that the taste fibres in the lingual branch of the fifth pair are furnished by the chorda tympani of the seventh pair after the latter leave the middle ear. Stimulation of these fibres arouses a sense of taste ; this not only places their function beyond doubt, but also proves that, apart from the stimulation at the periphery, there is a specific taste reaction in the brain. The fibres of the fifth pair are not connected with taste bulbs, for none are found over the area of their distribution. The taste bulbs are the essential nerve terminations of the glosso-pharyngeal nerve, and if this nerve be cut the bulbs degenerate. Motor power to the tongue is furnished by the hypoglossal or twelfth pair ; section of these nerves prevents an animal from masticating its food, the organ hanging helplessly from the mouth, and receives injury from the incisor teeth.

It is necessary for the purpose of taste that the substance should be dissolved ; this is one of the functions of saliva, and experiments on herbivora show that taste produces an abundant secretion from the submaxillary and sublingual glands, though not from the parotid.

SECTION 4.

The Cutaneous and Internal Sensations.

The sensations imparted from the surface of the body to the animal are not of one character only: touch is different from heat, cold is something apart from pain. These four sensations of *pressure* or *touch*, *heat*, *cold*, and *pain*, make up the complex, combined or uncombined, which composes the cutaneous senses. It is easy to realise the remarkably sensitive nature of the entire surface of the body. There is no part, excepting the horn of the feet or head, which does not give evidence of pain on being cut; there is no part, including the feet and horns, which is unconscious of touch or pressure. This sensory envelope is in the main protective, but it serves many other functions; some of these we have already studied under Respiration, Secretion, and Animal Heat; some have been referred to under the head of Muscle Tonus, on which much more remains to be said. But besides these, there are afferent impulses proceeding from the skin which indicate to an animal the position of its limbs, which direct its muscular efforts, enable it to judge of weight and resistance and, in conjunction with afferent impulses from muscles, initiate the changes which lead up to a muscular contraction. With none of these are we at present concerned, but only with those afferent impulses of common sensibility and pain proceeding from the skin to the central sense-organs, where their nature and character can alone be realised and distinguished, though the sensation is referred to the stimulated surface, and not felt in the brain.

In the matter of sensibility there is a great contrast between the surface of the skin and all that lies beneath it. Muscles, bones, and tendons, exhibit no ordinary sensibility; the same applies to the viscera, heart and lungs, liver, kidneys, and intestinal canal, which are partly or wholly without sensation. Under normal conditions the above structures, even when aroused by disease, are still devoid of touch, heat, and cold, though pain may be felt acutely.

Experiments made by Head and Rivers have shown that there are two sets of sensory skin-fibres—a deep and superficial. The former convey sensations of pain, and of marked heat and cold; the latter convey sensations of touch, and small differences of heat and cold. Touch sensations are divided into those of tactile localisation and tactile discrimination; these are conveyed by separate nerve-fibres—in fact, distinct fibres exist for all the cutaneous senses; those conveying pain do not transmit cold, and those transmitting cold do not convey heat. It is remarkable that touch, heat, cold, and pain senses are distributed over the surface of the skin in spots or dots. There are spots which are responsive to pressure, others to warmth, others, again, to coldness, and on suitable stimulation others feel pain. Maps showing the distribution of these four surface senses have been prepared in man, in whom alone their differentiation is possible. There is no reason to think that the same principle of distribution does not hold good for the lower animals.

Temperature-Sense.—Cold spots are more widely distributed than warm, which suggests that it is more necessary that the body should be made acquainted with the fact that it is cold than that it is hot. The feeling of warmth or cold depends upon the temperature of the skin, and not upon that of the body.

Pressure-Sense.—The distribution of the spots is wider than in those of the temperature-sense. The special nerve-endings connected with pressure are found in a ring around the hair follicles, in which position they are obviously most favourably situated for stimulation through the hair itself. In the hairless parts of the skin and muzzle special tactile corpuscles are found, and in the horse special nerve-endings exist in the foot associated with tactile sensibility. Tactile sensations play a very important part in the lives of animals. In the lips and muzzle, which correspond to the fingers of the biped, the touch organs proper are located (p. 299); these parts are endowed with exquisite sensibility, which enables the animal to be kept acquainted with the nature of its surroundings and the character of its food. The long feelers or hairs growing from the muzzle, face, and brow of the horse are in connection with nerves in the skin, and are valuable for tactile and consequently protective purposes. The 'cat hairs' on the general surface of the body are doubtless for the same purpose. The tactile sensibility of the foot, by informing the animal of the character of the ground it is travelling over, is useful, though not absolutely essential, in locomotion; nor is the tactile sensibility in the foot of the horse absolutely essential to its safety in progression, as is clearly proved by the results of plantar neurectomy.

Pain-Sense.—This is the most widely distributed of the cutaneous senses. It is distributed in spots, probably supplied by special fibres, though no special nerve-endings have been determined. Pain confined to the surface of the body can be readily located, but the localisation of interior pain is difficult; that of colic, for example, is referred to the abdominal wall. It is supposed in man that the explanation of the difficulty in localising interior pain is, that the segment of the spinal cord supplying the affected organ refers the pain to the skin region of the same spinal segment instead of to the organ. Painful sensations are of various characters—hence such terms as 'stabbing,' 'boring,' 'burning,' 'throbbing,' etc., to express the impression imparted. It is presumed that amongst the lower animals these different qualities of pain exist ; it is quite certain, for instance, that the pain exhibited by a horse during an attack of colic is very different from that shown when pus is forming in the foot. Of the nature of pain nothing is known. Its cerebral centre lies in the thalamus (see p. 491).

Muscle, Motorial, or Kinæsthetic Sense.

The term 'muscle-sense' has been employed to describe several allied, though quite distinct, conditions to which the muscles directly or indirectly contribute. It covers such questions as a knowledge of the existence of muscles and of their position ; the position of the limbs at rest and in motion ; the proper and orderly contraction of muscles, and of the correct grouping of sets of muscles—viz., muscular co-ordination—both for locomotion and for equilibrium. It goes further : it deals with weight and the resistance offered in muscular contractions, and in conjunction with touch and sight it forms conceptions of space, distance, and height. To many it has appeared that the grouping of this set of complex functions under the term 'muscle-sense' is liable to prove misleading, for there is no evidence that in all cases the muscles play a predominant part in the various phenomena ; in consequence the term **motorial** or **kinæsthetic sense** is considered a more suitable designation.

Sherrington has shown that muscles receive a rich supply of afferent nerves, one-half to one-third of the nerves in muscle being of this nature. These sensory fibres terminate in special nerve-endings in the muscle or its tendon. These endings are known as **muscle-spindles** ; they are believed to be activated by variations in the tension of the muscles. The proof that these spindles are sensory in nature is afforded by the fact that when the inferior roots of the spinal cord are divided no degeneration of them occurs. It is through these fibres, which enter the cord by the dorsal roots and travel both to the cerebrum and cerebellum, that the brain is made acquainted with the condition of the muscles. The cerebellum, through its connection with the semicircular canals of the internal ear, enables a judgment to be formed of the position of the body in space, and its relationships to its surroundings. These are communicated to the cerebrum, from which impulses pass from the centre representing the muscles to the muscles themselves. It would appear that centres must exist in the cord by which at least part of this work is carried out, for it has been shown (p. 449) that after it has been divided in the dog, and sufficient time has elapsed, muscular co-ordination is re-established, though no communication with the brain is possible. There are other reasons which have also been mentioned which suggest that the cord of the lower animals is capable of automatic activity in the matter of muscular movements, being stimulated by the constant inpouring of sensory impulses through the muscle-afferents.

Deep pressure sensibility, such as arises from joints, and the sensory impressions arising in the skin and subcutaneous tissues of joints, are intimately concerned in the kinæsthetic sense. It is probable that it is particularly in operation in determining weight and resistance, and it would appear to be well developed in draught-horses. The horse employed in ' shunting ' knows in a second the amount of effort required to start truck-loads of varying weight. This information is transmitted through the skin under the collar and over the large joints, especially the shoulder, hip, and stifle.

The importance of ' muscle sense ' in provoking a muscular contraction is shown by the pseudo-paralysis which follows division of the sensory nerves. This operation causes no loss of power, but it cuts off all afferent impressions from the muscles of the part ; the dog drags his legs, the arm of the monkey hangs helplessly, in spite of the fact that in neither case have the motor mechanisms been interfered with. The same is seen in the horse on dividing the superior maxillary branch of the fifth nerve ; the animal is unable to use his lips as a prehensile organ, though they possess their full share of power.

Judgment of distance, the relationship of space, and the muscular co-ordination connected with equilibrium, are indefinably mixed up with muscle-sense, vision, and the internal ear. The extraordinary judgment shown by horses in jumping, both as to height and distance, is mediated through this channel. Some animals never acquire it, are clumsy, make but little effort to rise, or, if tired, none whatever ; others are willing, but their judgment is defective, and the muscles are directed to perform unnecessarily powerful contractions ; a third group, confident in their powers and judgment, and unwilling to do more than is necessary, run matters so fine that it requires a fall to remove their pride. Muscle-sensation is very evident in the tired animal, and is probably the only occasion, apart from lameness, in which a horse is conscious of possessing limbs.

Muscle-sense has been referred to in the chapter on the Muscular System (p. 390), Nervous System (p. 470), and will be again met with in dealing with Locomotion.

Hunger.

The sensation of hunger is referred to the stomach. It has been supposed that it is excited by the approximation of the walls of the organ, but animals may exhibit hunger at a time when the stomach contains food—for instance, the horse and the rabbit. Nothing is known of the nervous mechanism connected with this condition. It is one of the senses under the control of a lowly organised part of the brain, for a dog without its cerebrum shows the usual signs, though obviously it cannot be associated with any conscious knowledge of want. The length of time animals will withstand starvation is dealt with at p. 363. A horse in good condition has been known to live thirty days provided water be given ; but an animal in poor condition to start with has died in half that time. The remarkable period during which sheep have lived without food has been mentioned at p. 363, and a similar fact has been recorded in the pig ;* the animal was buried for sixty days in a landslip, and was recovered alive, having lost in that time 120 pounds in weight. It is not known why eating gives practically *immediate* relief to all the symptoms of hunger, for it is obvious that the food ingested can be of no use until absorption has commenced.

Thirst.

Very little is known of the subject of thirst—not even why the sensation is referred to the pharynx. It has been supposed that the glosso-pharyngeal nerve has special nerve-endings in the pharynx, which are stimulated when the water content of the body falls below a certain point; for if the palate be moistened thirst is allayed, while filling the stomach with water through a fistula does not at once control the desire for fluid. If a horse be ‘ sham watered ’—viz., with a fistula in the œsophagus—he leaves off drinking, after a few swallows, as if satisfied, and then starts again as the pharynx gets dry (Colin).

There is a constant loss of water occurring in the body-fluid through respiration and the various secretions, such as sweat, urine, milk, and digestive juices. Some of the fluid of the latter may be reabsorbed; especially is this likely to occur in such bulky secretions as saliva in the herbivora. The requirements of an animal for water are constant, though varying with the season and the nature of the food. In summer the loss by sweat in working horses, and the extra transpiration by the air-passages, all have to be made good. Animals receiving dry food require more water than those on green herbage. According to Colin's researches, 4 kilogrammes (8·8 pounds) of hay require 16 kilogrammes (35·2 pounds) of saliva, and the fluid for this has to be drawn from the blood. When 'roots' form a portion of the daily diet the amount of water consumed becomes considerably reduced. So much is this the case that sheep fed on roots and succulent food are not watered; and the rabbit receiving succulent food does not drink. The assumption that neither of these animals requires water is at once disproved by placing them on a diet of dry food. Purging, hæmorrhage, and diabetes, prove severe sources of water-loss to the tissues.

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* Martell, Transactions of the Linnean Society, vol. ix.

Thirst is badly borne by animals, certainly by the herbivora. The capacity for work with horses falls off considerably, and as the fluid contents of the digestive canal and tissues is drawn upon the abdominal wall contracts, and the animal wears a pinched and anxious look. Under these conditions in war, horses have been known, on obtaining access to water, to drink until they died, presumably from rupture of the intestines.

The ordinary exhibition of thirst in stabled animals is at once recognised by the trained eye. The horse that pricks his ears and gazes intently when he hears the sound of a bucket, and the peculiar motions of the mouth of the thirsty horse at the sight of water, are indications as unmistakable as speech.

Deprivation of fluid is productive of intense suffering. Hunger may be taken philosophically, but not thirst; one extinguishes life in a few days, the other in a few weeks. So essential, indeed, is the regular renewal of fluid that the sick animal, though turning from food with disgust, never fails, but in one disease, to consume fluid; during the existence of acute abdominal pain a horse will not drink, yet the leathery dryness of the mouth suggests intense thirst.

SECTION 5.

Hearing.

The Nature of Sound.—When a body is made to vibrate, its vibrations are communicated to the adjacent air, and give rise to waves which travel at a definite rate ; when these reach the ear they act upon its structures so as to lead to the sensation of sound. The vibrations which constitute the waves take place to and fro along the direction in which the wave is travelling ; in this respect sound differs from light, whose vibrations are transverse to the direction of propagation.

In comparing one sound with another we are conscious of only three possible differences between them : they may differ in loudness, pitch, and quality. Of these, loudness is dependent on the *magnitude* of the to-and-fro motion of the vibrating particles whose movements transmit the sound ; a loud sound means a large wave. Pitch, on the other hand, depends on the *frequency* of the vibrations, a high note implying rapid vibrations, or a shorter wave-length. Sounds may be simple or compound. The vibrations of a tuning-fork give rise to a typically simple sound, of varying loudness or pitch, but possessing little quality. Most vibrating bodies do not give rise merely to such simple vibrations, but set up a variable series of different wave-lengths along with their fundamental simple vibration. Thus, most sounds consist of a fundamental tone, accompanied by more or less of these other tones—the *partial tones*, *overtones*, or *harmonics*, as they are termed. The quality of a sound depends upon these harmonics ; where they are absent the tone is thin, where they are present they give richness, and confer on it that ‘ character ’ which enables us to recognise one musical instrument from another by the mere sound it emits. Those sounds which are grouped under the general term of ‘ musical ’ result from the regularity of their causative vibrations, and the definiteness in wave-length of the latter. *Noise* is essentially the result of the absence of this regularity and definiteness. There is usually no difficulty in discriminating noise from musical sounds, but the one may merge into the other, as in the case of the noise of street traffic when near to it, and the musical humming tone it produces when heard from a distance. From observations on the human subject it has been ascertained that the smallest number of vibrations audible are about thirty per second, whilst the average human ear can recognise up to 30,000 vibrations per second. It is undoubted that some animals can recognise a smaller number of vibrations than thirty per second. Galton has shown that the cat is capable of recognising sounds inaudible to the human ear.

External Ear.—The vibrations of sound are collected by a freely moving funnel-shaped body or external ear; it is composed mainly of cartilage, which is curved and hollowed out in such a way as to form a good collector, while several muscles enable it to assume considerable changes in direction. The two chief directions taken by the ears are backwards and forwards; judging from the behaviour of many horses in carrying one ear backwards and the other forwards, it would appear that they are capable of hearing and appreciating sound in two opposite directions at one and the same time. The funnel formed by the external ear leads somewhat indirectly to a canal known as the external auditory meatus; in and around this is found an unctuous secretion, and above it, in the funnel of the ear, are many hairs, which are for the purpose of protection.

The **movements of the ears** give evidence of what is passing through the mind of an animal; this observation is as old as Pliny.* The ears of the horse are turned well to the front and closely pricked—viz., the points approximated, when he is attentive, whether the attention be devoted to a something he is alarmed at or pleased with. The ears are laid back on the poll in sourness of temper and in vice; they are moved rapidly to and fro when a horse is anxious either from impending danger or other cause; one ear carried forward and the other backward, or both turned backwards, is considered the sign of a good stayer and willing worker; while drooping ears are indicative of muscle-fatigue or natural flabbiness.

Whatever part those remarkable sacs, the **guttural pouches** (confined solely to solipeds), are intended for, it is probable, from their anatomical connection, that they take some share in the sense of hearing, perhaps that of supplying the needful amount of air to the middle ear (Fig. 180). The actual use of the guttural pouches is involved in obscurity, but they may provisionally be considered as part of the middle ear. In man acuteness of hearing is enhanced by listening with an open mouth; the fact that the horse cannot breathe through the mouth may explain the presence of these large air-sacs beneath the skull; in other words, they are probably associated with acuteness of hearing, and in this capacity act as resonators. The air enters the guttural pouches during swallowing and during expiration; in the latter respect the pouches resemble the facial sinuses.

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* It is rather remarkable that the expressions of the mind in animals should be conveyed through opposite poles of the body—*i.e.*, the ears and tail. In dog, cat, and horse, the movements of ears and tail each tell their own distinctive story.

Structure of the Ear.—At one end of the external auditory canal is a piece of membrane stretched completely across it, known as the *Tympanum;* it separates the external from the middle ear (Fig. 181). The *Middle Ear* is on the inner side of the tympanum; it consists of a cavity containing a chain of very small bones, which stretch like a bridge across the space from the tympanum to the third or internal ear. The middle ear, like the external, is in communication with the air by means of a passage known as the *Eustachian canal*, which opens into the pharynx. The tympanum has, therefore, air on both sides of it, the object of which is to ensure that the atmospheric pressure on either side is equal, and so permit its free swing. The air ordinarily finds its way into the Eustachian tube during the act of swallowing, and by the same channel it is conveyed to the guttural pouches. The *Tympanum* is concave towards the external ear; in the middle ear the handle of the *malleus* is fixed to the central bulging part of it, and as this bone articulates with the *incus*, and the latter with the *stapes*, any alteration in the shape of the drumhead, such as is produced by the vibrations of sound, causes the bridge of bones to move; their movement is further assisted by two small muscles which are attached to them.

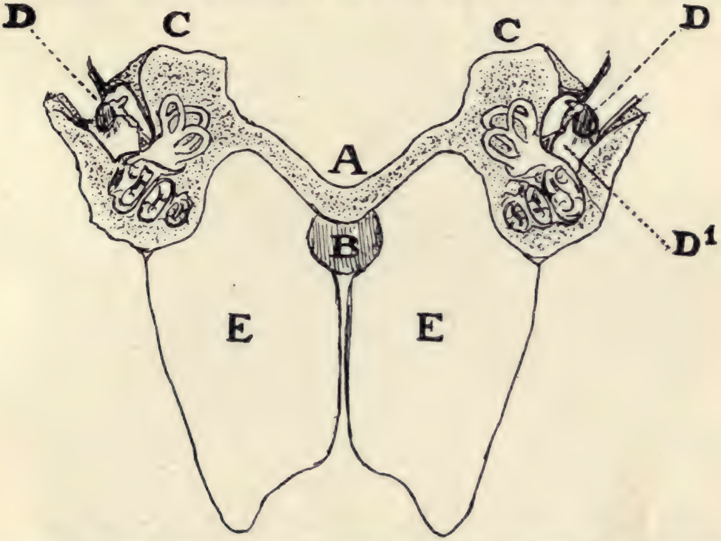

FIG. 180.—DIAGRAMMATIC SECTION ACROSS THE SKULL, INCLUDING BOTH PETROUS TEMPORAL BONES, SHOWING THE RELATIVE POSITION OF THE EAR TO THE GUTTURAL POUCHES.

A, Base of cranium; B, insertion of a muscle of the neck; C C, petrous temporal bones; D D, external ear; D′, middle ear; E E, guttural pouches. The communication of the latter with the pharynx below and the middle ear above has to be imagined (see Fig. 181). The figure also shows, though purely diagrammatically, the position of the semicircular canals and internal ear in the living animal.

The *Internal Ear*, known as the *labyrinth* (Fig. 182), is composed of the *semicircular canals*, the *vestibule*, and the *cochlea ;* these are contained in a solid piece of bone in which two small foramina or windows exist, one known as the *fenestra ovalis*, the other the *fenestra rotunda ;* the base of the stapes or third bone of the ear is attached to the membrane which covers the fenestra ovalis.

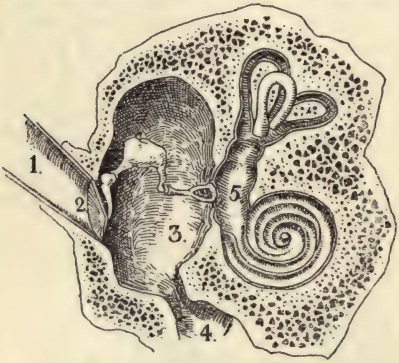

Fig. 181.—Diagrammatic Section of the Horse's Ear.

1, External auditory canal; 2, the tympanum; 3, chain of bones across the middle ear; 4, the Eustachian tube; 5, the internal ear; the number is on the vestibule, above which may be seen the semicircular canals, while below is the cochlea.

All three parts of the *labyrinth* communicate, but it is quite certain that all three do not take an equally active part in hearing. The cochlea alone is the essential organ of hearing. The whole of the labyrinth is lined by a membrane containing a fluid known as the *peri-lymph;* this peri-lymph has free access to all parts of the inner ear. Within this membrane is a membranous labyrinth, the counterpart of the semicircular canals and vestibule, and this also contains fluid known as *endo-lymph*.

Two windows exist in the bony labyrinth. The base of the stapes lies over one of them, and between the stapes and the peri-lymph is the membrane which lines the internal ear. Every movement of the tympanum causes the bony bridge to oscillate, and every oscillation of this thrusts the stapes against the membranous window, and so sets up oscillations in the peri-lymph which are transmitted throughout the internal ear.

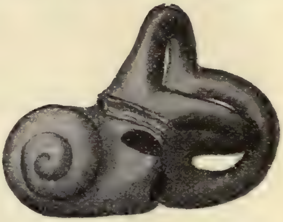

Fig. 182.—The Labyrinth (Edmunds).

The semicircular canals are to the right, the cochlea to the left; both windows may be seen, the *fenestra rotunda* being the lowermost. The groove across the body of the organ lodges the auditory nerve. The figure is enlarged.

The *cochlea* resembles in appearance the shell of a snail, its interior being divided into three spiral channels, which wind their way from base to apex like a circular staircase. The number of twists in the cochlea is two and a half; the axis around which these wind is composed of soft bone, having canals up which the auditory nerve travels. If a spiral of the cochlea be cut across (Fig. 183) the three canals it contains are seen. These are divided by septa; one septum, known as the *lamina spiralis*, separates the upper canal or *scala vestibuli*, from the lower one or *scala tympani*. The third, or middle canal, is of a triangular shape and called the *cochlear canal ;* it contains the essential organs of hearing, and lies between and to the outside of the other two. The roof of the cochlear canal is formed by a piece of tissue known as the *membrane of Reissner*, while its floor, on which is situated the essential organs of hearing, or *Organ of Corti*, is formed by the *membrana basilaris*, which connects the outer wall of the cochlea to the lamina spiralis; a cover to the organ of Corti is formed by the *membrana tectoria*. The cochlear canal is the continuation of the membranous labyrinth. The upper passage of the cochlea—*i.e.*, the scala vestibuli—is continuous with the lymphatic peri-lymph space of the vestibule, whilst the scala tympani, or lower passage, ends at the base of the cochlea in a blind extremity in which is a membranous window, the fenestra rotunda, which separates the scala tympani from the cavity of the tympanum. The cochlear canal terminates suddenly at the summit of the cochlea, and at this point the two scalæ, which in their windings have been decreasing in size from base to apex, meet and communicate by a small opening, the *helicotrema*, and the fluid of the one is thus in connection with that of the other.

Organ of Corti.—This consists of a triangular-shaped tunnel (Fig. 183), the base of which rests on the basilar membrane; the tunnel is composed of certain rods arranged side by side, inclined from both sides towards each other, and meeting superiorly like an inverted **V**. At this point the rods, known as the rods of Corti, fit into each other in a peculiar manner. Flanking either side of the tunnel are certain cells of two distinct kinds; those nearest to the tunnel are somewhat flask-shaped, and having hairs growing from their summit, are spoken of as the *inner* and *outer hair cells*; external to the outer hair cells are some tall conical cells known as *Hensen's cells*. The auditory nerve ascends the axis of the cochlea, giving off branches which in their passage ramify over the lamina spiralis, at the outer edge of which the above-described organ of Corti exists; having reached this the fibres lose their medulla, and the naked axis cylinders pass into the cells flanking the triangular tunnel, some fibres crossing the tunnel to reach the cells on the opposite side. How the nerve terminates in the hair cells—for it is to these that it is distributed—is unknown, but that the hair cells are the organs of hearing is undoubted; Hensen's cells are probably only of a nutritive nature and unconnected with auditory impulses.

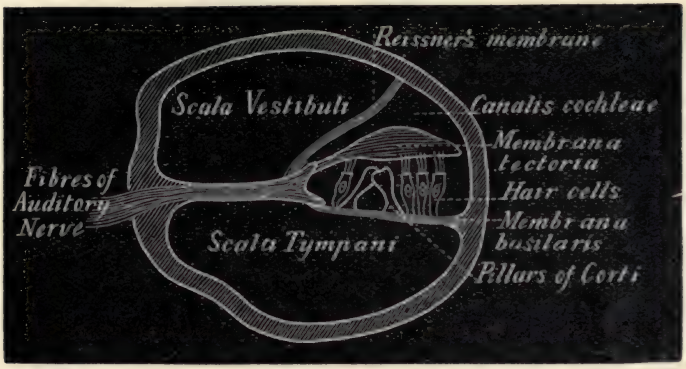

FIG. 183.—DIAGRAMMATIC TRANSVERSE SECTION OF A TURN OF THE COCHLEA.

Auditory Sensations.—Any analysis of these is hardly necessary in a work dealing with the lower animals ; we have no direct evidence that they understand or appreciate the difference between music and noise ; a dog will howl at one as readily as another. At the same time it is certain that animals can learn to recognise sounds and associate them with certain ideas, as, for instance, the commotion and excitement amongst the horses of a regiment when the trumpet sounds ' feed,' and again the recognition by a dog of its master's voice. Further, we have undoubted evidence that sounds which are so feeble as not to affect the human ear are readily perceived by some animals, so that the acuteness of their sensations is greater than that of our own, though their capacity for the enjoyment of music is absent or extremely small.

The vibrations set up in the tympanum are communicated to the chain of bones, the stapes of which, through the fenestra ovalis, imparts a push to the peri-lymph of the labyrinth ; this fluid transmits the impulse through the vestibule, and from here into the scala vestibuli of the cochlea. The vibrations ascend the spiral staircase, and set in motion the membrane of Reissner, which causes the lymph in the cochlear canal to vibrate ; when these vibrations reach the summit of the cochlea they enter the scala tympani through the helicotrema. The lymph in this canal is now set in motion, with the result that the basilar membrane, on which the organ of Corti rests, is affected, and the vibrations are ultimately lost at the blind extremity of the canal, whose membrane is pushed outwards at the fenestra rotunda. Every push inwards at the fenestra ovalis causes, therefore, a push outwards at the fenestra rotunda. During the time the vibrations are crossing the cochlear canal from one scala to another the organ of Corti is affected, and by means of the auditory nerve the impulse is conveyed to the brain. It is in the organ of Corti, with its nerve-endings, that the complex sounds which make up even a single note of music are analysed, and this analysis was at one time supposed to be effected by the rods of the organ, which were believed to vibrate to their own particular tone, in the same way as a tuning-fork will pick out its own tone from sounds in its vicinity and vibrate to it. This view, tempting as it is, is negatived by the fact that the rods of Corti do not exist in birds, and it has therefore been supposed that the vibrations to the nerves terminating in the organ are set up by the vibration of the basilar membrane on which the organ is built, or by the tectorial membrane which covers them, but the question is far from settled.

Semicircular Canals and Vestibule.

We have seen elsewhere (pp. 481, 522) that the eighth pair of cranial nerves consists of two roots, dorsal and ventral, both distributed to the internal ear, but both are not concerned in the sense of hearing. The dorsal root alone is distributed to the cochlea, the ventral root passes to the vestibule. In consequence the nerve has been distinguished as the cochlear and vestibular division of the auditory nerve. The cochlear division is exclusively devoted to the sense of hearing, the vestibular division to the function of maintaining the equilibrium of the body. The vestibular nerve is connected with the cerebellum, the nuclei which control the muscles of the eyeball, and with motor cells in the cord. It is not directly connected with the cerebrum. In the internal ear it is connected with the semicircular canals and the vestibule.

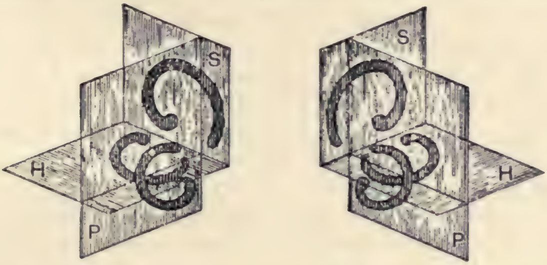

FIG. 184.—THE SEMICIRCULAR CANALS (DIAGRAMMATIC) (EWALD).

H, Horizontal canal; S, superior vertical canal; P, posterior vertical canal. The two horizontal canals are in the same plane. The superior vertical canal of one side is parallel to the plane of the posterior vertical canal of the opposite side.

The **semicircular canals** are three in number, and so arranged that their three planes are placed at right angles to each other, two being vertical and one horizontal (Fig. 184). Their positions in the living animal are shown in Fig. 180. Within each bony canal is a membranous counterpart separated by a fluid known as *peri-lymph*, while within the membranous organ is another fluid described as *endo-lymph*. Each canal terminates in a swelling known as the ampulla. The semicircular canals open into the vestibule by five openings—some say four (Sisson). Within the vestibule are two membranous sacs, the *utricle* and *saccule ;* the former communicates with the semicircular canals, the latter with the utricle and cochlea. These sacs, together with the ampullæ, contain the hair-like processes representing the sensory nerve organs of the vestibular division of the seventh nerve.

These hair cells arise from definite areas of the utricle and saccule, and project into a mass of mucus containing, especially in the horse, fine solid particles of carbonate of lime, known as **otoliths.** The vibrations of the endo-lymph set these hair cells in motion, and so convey impulses to the brain. The vibrations, however, are not sound vibrations, but such as are produced by the movements of the head up and down, right and left, the fluid in the semicircular canals concerned being readily influenced by such movements. The displacement of the fluid impinges on the nerve-endings, and starts impulses to the cerebellum. By means of these impulses the brain is informed of the position of the body, more particularly, perhaps, movements of rotation, and co-ordination becomes possible under the influence of the cerebellum. There are other effects upon voluntary muscle; it is supposed that from the labyrinth a constant outflow of impulses is occurring, which maintains them in a condition of tone, for it can be shown experimentally that the destruction of the semicircular canals causes the loss of muscular tone on that side, and in case of death delays the appearance of rigor mortis. Among their other functions, the semicircular canals may be regarded as muscle-tone organs. The functions of the utricle and saccule are probably connected with the position of the body when at rest, and of forward movement not associated with orientation. In these organs the hair cells are supposed to be affected by actual mechanical stimulation by the otoliths in their vicinity.

The function of the labyrinth, to quote the words of Sherrington, is to keep the world right side up for the organism, by keeping the organism right side up to the external world. It is by means of the semicircular canals that an animal is made acquainted with the direction in which its body is travelling, forward or backward, right or left, up hill or down, or in the movements which occur in jumping. Another function connected with the semicircular canals is that of the control of the ocular muscles and the maintenance of a horizontal pupil. It is no wonder, considering their extraordinary importance, that they are securely lodged within the substance of the hardest bone in the body.

Stimulation of the semicircular canals produces giddiness and movements of the eyes. If the *membranous* canals be destroyed in a pigeon, the resulting phenomena depend upon the position of the canal which has been injured. If the horizontal canal, the head oscillates in a horizontal plane; if the vertical canals be damaged, forced movements occur in a vertical plane; standing and locomotion become impossible. If all three canals be destroyed, violent inco-ordinate movements result, the animal turns somersaults, the head is twisted, the eyeballs roll from side to side, and special measures have to be taken to prevent the creature killing itself through its own violence. These violent symptoms pass away in due course, and the animal is able to stand and walk, though the process has to be learnt. Vision here gives the sense of direction and spatial relationship, for if the eyes be covered farther progress is impossible.

CHAPTER XVI

LOCOMOTOR SYSTEM

SECTION I.

Muscles, Joints, Tendons, Ligaments.

Muscles and Joints.—The structure of muscle, its innervation, and the phenomenon of a muscular contraction, have been studied. It is here intended to examine the muscles at work, and ascertain what they are capable of effecting, and how they effect it. Speaking broadly, the skeleton is clothed with muscle; there are exceptions, such as the face and the limbs below knees and hock, where the framework is uncovered, but generally the bones are clothed, the muscular covering of the limbs becoming progressively lighter from above to below. The scapula and humerus, the pelvis and femur, are buried beneath a mass of muscle; over the radius and tibia the muscular structure is much less in bulk, and immediately at the knee and hock it suddenly ends. The movements of the limbs of quadrupeds are of a simple character. Keeping entirely to solipeds, it consists of a to-and-fro pendulum motion, and a limited movement in an outwards and inwards direction. This is infinitely more simple than in those animals furnished with a paw or hand. The limbs have to be flexed and extended, abducted and adducted, and both in the fore and hind legs these are carried out entirely by the muscles clothing or attached to the scapula and humerus, pelvis, femur, and tibia.* Speaking broadly, no muscles originate below the

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* A definition of the following terms employed in limb and joint movements may be desirable:

Flexion and Extension refers to either joints or limbs. To flex a limb is to bend it; to extend a limb is to straighten it. Nevertheless this does not cover the entire ground; the foot, for instance, during the movement of flexion causes the pastern to become extended—viz., straightened. Conversely, when the foot is extended, the pastern is bent or flexed.

Abduction and Adduction.—These terms only apply to limbs. A limb is abducted when it is carried away from the middle line of the body. Similarly, it is adducted when drawn towards the middle line. The amount elbow or stifle joints. This being so, it is evident that movements of the upper part of the limbs are automatically followed by movements of the lower parts.

Flexion and Extension.—It is usual to picture muscles at work from the appearance presented on the dissecting-room table ; valuable as this is, it does not tell the whole story. It is only when muscles function that the fundamental principle is grasped that they are really never idle, and that even when not engaged in performing the more active duties for which they exist, they are still part of the animal machine, and engaged in the work of muscle co-operation. Flexion, extension, abduction and adduction, are not the exclusive function of individual muscles. A muscle is not, for instance, exclusively engaged as a flexor or extensor : it may be actively employed in flexion, or passively employed in extension ; it may be actively engaged in extending one joint, and actively engaged flexing another ; it may be actively flexing one joint, and automatically flexing its neighbour ; it may be passively employed in extending one joint, and when active act as a flexor of another. Examples of these will now be given, for if the machine at work is to be correctly visualised, the ground-work for this is the facts above stated.

1. *A muscle may be a flexor when contracting, and an extensor when not active.* A good example of this is the flexors of the fore-limbs which, when not contracting, are maintaining the elbow-joint firmly extended. Another is the *biceps brachii* (*flexor brachii*), which when actively contracting flexes the elbow-joint, and when passive is assisting, by means of a strip of tendon to the *extensor carpi radialis* (*extensor metacarpi magnus*), in keeping the knee firmly extended.

2. *A muscle may be engaged actively at one and the same moment in extension and flexion.* This is met with in the *superficial digital flexor* (*flexor perforatus*) of the hind-limb, which extends the hock-joint and flexes the pastern.

3. *A muscle may be actively engaged flexing one joint and*

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of abduction and adduction of the limbs is very small. On the one hand, it reaches its maximum in a 'cow-kicker,' and on the other in a horse that 'brushes' from defective conformation, but especially in a 'weaver.'

Rotation is a term limited to joints, and the only joints in the limbs of the horse which can rotate are the shoulders and hip. Rotation of the stifle is produced in the hock and carried out in the hip-joint.

It is obvious that in all movements of flexion, extension, abduction, adduction, and rotation, the act is not an isolated one ; the movements must work at least in pairs, and sometimes the entire series is employed. Take, for example, a horse 'cow-kicking ': the limb must first be flexed, then forcibly extended, and at the same time abducted. To admit of this there must be rotation of the hip, and to allow the limb to recover its position adduction must follow.

automatically flexing its neighbour. The muscles which flex the stifle-joint automatically flex the hip.

4. *A muscle may in flexing one joint flex several others.* This is met with in the flexors of the fore-limbs, which flex knee, fetlock, pastern, and foot, at one and the same contraction.

5. *A muscle may be passively engaged extending one joint and actively employed in flexing another.* An example of this is the *tibialis anterior* and *peroneus tertius* (*flexor metatarsi*), which are passively engaged by means of the cord which runs through its substance in maintaining the stifle extended, and when that joint is flexed is actively engaged in flexing the hock.

6. *Two parallel muscles, with a common tendon of origin, may act in opposite senses.* This is met with in the *tibialis anterior*, *peroneus tertius*, and *anterior long digital extensor* (*flexor metatarsi* and *extensor pedis*) ; the one extends the foot, the other flexes the hock.

7. *A muscle may both passively and actively be an extensor only.* An example of this is the gastrocnemius muscle, which, whether the foot be on or off the ground, is an extensor of the hock.

It is possible for a muscle to be so anatomically situated as to appear to act as an extensor of one joint and a flexor of another, yet when the muscle is acting in the living animal it may be found to act only as a flexor, and never as an extensor. Sherrington has shown that this is the case with the *semitendinosus* muscle of the cat, which is so situated as to act as a flexor of the knee (stifle) and an extensor of the hip joint ; but experimentally it can be shown that the muscle always flexes the knee, and never extends the hip, for the reason that the hip flexor contracts at the same moment, and neutralises its action on that joint.

It has already been pointed out (pp. 391, 402, and 458) that even when the muscles of the body are apparently not acting they are in a condition of slight contraction, which is necessary for the maintenance of the standing attitude, and that it is only during the time the animal's weight is actually off its legs that the muscles can be considered to be at rest.

When a muscle contracts its antagonist is relaxed, and the nervous channel through which this is effected has been described under the head of ' reciprocal innervation ' (see p. 456). Where muscles act on a single joint as a flexor and extensor the reciprocal nervous mechanism is easily understood, as the two muscles are direct antagonists. But when muscles are not exclusively devoted to one joint—in fact, affect two or more—the nervous mechanism is not so simple, for the reason that flexion at one joint may lead to extension at another. An example of this has already been given ; the *semitendinosus* muscle is only permitted to act as a flexor of the knee (stifle) of the cat, and not as an extensor of the hip, and to secure this the latter joint is fixed by a contraction of its flexor muscles. In such cases the nervous mechanism is *identical*, not reciprocal, for the flexors of the hip contract in order to prevent extension of this joint at the same moment as the semitendinosus contracts and flexes the stifle.

The condition revealed by this experiment is that flexor and extensor muscles, true antagonists, may contract together, co-operate, in order to fix a joint, so that another joint may be more effectively acted upon. Similarly, two extensor muscles may be actively employed some distance from each other in fixing the joint of a limb ; they are not true antagonists, they are both extensors, and they act at the same moment : they are spoken of as ' partial antagonists.' The best example of this is afforded by the gastrocnemius muscle, which always acts as an extensor, whether during standing or in active movements, yet its origin from the femur is such that it might flex the stifle. It never flexes the stifle, for the reason that the muscles of the patella keep the stifle extended at the time the gastrocnemius is acting by keeping the hock extended. The patella and gastrocnemius muscles are partial antagonists : they contract together and relax together, and by so doing ensure that one joint is kept fixed in order that a muscle crossing it may act better on another joint. The innervation such muscles receive is identical (see p. 456).

When muscles have a muscular origin and a tendinous insertion, the direction in which their contraction occurs is from muscle to tendon ; but when muscles are fleshy throughout, such as the long muscles found in the dorsal region, they may act from either end—for instance, in the group referred to they act from the neck end in kicking, and the croup end in rearing (Figs 214, 215).

Tendons and Ligaments.—The chief function of ligaments is to hold bones in position. The greater the necessity for joint freedom, the fewer and simpler the ligaments. The shoulder-joint, for instance, has no special lateral ligaments. The range of motion is too considerable for these, so that the tendinous insertion of the muscles takes their place. There is very much less motion in the hip, and the ligaments are centrally placed. With the other joints they are laterally situated, but from knee and hock to the foot a ligament seems to have been put in wherever space not otherwise occupied existed. Ligaments are also employed for holding floating bones like the patella and sesamoid in position. They knit together the various segments of the spine, and one of peculiar structure supports the head and neck. Ligaments may also run to tendons to enable the muscle to be partly cut off during the standing attitude. Two to the flexors of the lower limb of the horse undoubtedly assist the animal to sleep in the standing position while the muscles rest. They are known as **check ligaments.** Another kind of ligament peculiar to quadrupeds is a **tendo-ligament**—*i.e.*, a muscle with a tendon running completely through its substance from origin to insertion, which, when the muscle is not actively contracting, acts as a ligament, and when it is contracting plays its normal part of tendon. We shall see that this mechanism is employed both in the fore and hind legs for the purpose of maintaining a standing attitude with as little muscular strain as possible. A muscle may furnish a ligament to another muscle in order to afford it support. This is shown in the ligament detached by the *biceps brachii* (*flexor brachii*) to the *extensor carpi radialis* (*extensor metacarpi magnus*). A variation of this is a muscle detaching a ligament to a bone which is considerably out of its path—for instance, the ligament detached by the large *biceps femoris* (*triceps abductor femoris*) to the calcis.*

The elasticity of tendons and ligaments is considered later (p. 607). This feature has proved a fruitful source of difference of opinion, and the matter is by no means agreed upon.

The elasticity of muscle has been dealt with at p. 401, and to form a conception of what occurs to tendons under the influence of strain, the elastic property of muscle must not be lost sight of. Nothing could well be more unlike in appearance, texture, and general physical characters, than muscle and tendon. Yet the soft, pulpy, friable material does not tear in the living animal, while the tendon attached to it may be torn apart. The only locomotor muscle in the horse's body which shows a disposition to rupture is the *flexor metatarsi*, and such a lesion is so rare that many have never seen it.

Colin tested the breaking-strain of muscles removed from a horse which had just been destroyed. The great extensor of the metacarpus broke at a tension of 988 kilogrammes (2,173 pounds); the flexor perforans of the fore-limb at 685 kilogrammes (1,507 pounds); and the flexor of the arm at 973 kilogrammes (2,140 pounds). In the hind limb the extensor pedis muscle broke at 415 kilogrammes (913 pounds), the flexor of the metatarsus at 924 kilogrammes (2,032 pounds), and the flexor perforans at 510 kilogrammes (1,122 pounds). The extensors of the metatarsus ruptured at 616 kilogrammes (1,355 pounds), 687 kilogrammes (1,511 pounds), and 983 kilogrammes (2,162 pounds) respectively, but the muscles are not mentioned by name. It will be observed that the breaking-strain of the extensors is much higher than that of the flexors, that of the extensor of the metacarpus being nearly one ton. In the hind-limb there is a marked difference between the breaking-strain of the extensor pedis and flexor metatarsi muscles, though the two have a common tendon of origin. Finally, the relatively low breaking-strain of the flexor muscles is very evident. If the chief flexor of the fore-limb—a muscle which perhaps does half the work in connection with propelling the body in the gallop—breaks at a tension of 1,507 pounds, we may be sure from this that the breaking-strain of its tendon is correspondingly low. As a matter of fact, muscular rupture during life is rare, and it may be urged that such *post-mortem* observations do not represent what occurs under the living condition. That is certainly true; nevertheless it is suggestive that the low breaking-strain of the flexor muscles corresponds with the frequency with which during life the flexor tendons are sprained.

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* Anatomists are responsible for the confusion existing in muscle nomenclature. Where possible, the writer has followed Sisson in modern terminology, inserting the known equivalent in brackets. There are six names for the biceps femoris muscle!

Levers.—The muscles are attached to bones, and the latter form various angles with each other, which are opened and closed during progression. The mechanical aid introduced in order to effect this is the lever. Levers are of three orders, depending upon the relative position of the power, fulcrum, and weight. A *lever of the first order* is mainly a lever of extension, the power being at one end, the weight at the other, the fulcrum between. A good example is the extension of the head on the neck; the weight is the head, the power lies in the neck, the fulcrum is the joint between the head and neck. A *lever of the second order* is not common in the body. The weight lies in the middle, the fulcrum and power at each end. When the fore-foot is on the ground supporting weight, the foot is the fulcrum, the body through the elbow-joint is the weight, the power lies in the biceps muscle acting on the ulna. A *lever of the third order* is the lever of speed and flexion. In it the power lies between the fulcrum and weight. In the flexing of the arm the biceps is the power, the fulcrum lies above it in the elbow-joint, the weight lies below—viz., the weight of the limb. This is a lever which sacrifices power for speed; it is therefore wasteful, but necessary in the limbs.

Function of Muscles.—The muscles of the skeleton have a twofold function to perform—they move the body and they maintain its attitude. Accordingly, so long as the animal is not actually lying down, the muscles are in constant action, though the effort required to maintain attitude is less exhausting than that attached to moving and carrying weight. **A standing attitude** is maintained by the flexible limbs being rendered rigid, and this is effected by the muscles keeping the joints locked. For this purpose they receive a constant stream of impulses, and if these are withdrawn for ever so brief a period, the body falls under its own gravity.

It requires a greater muscular effort to maintain a standing attitude in the fore than in the hind legs, owing to the fact that the fore-limbs are not attached to the body by any joint, and are solely dependent on masses of muscle for support. When a horse sleeps in the standing attitude, his muscles not infrequently lose their tonic impulses, and he falls, but always front foremost, never hind foremost, and never in a heap. Long before his knees have reached the ground the muscles have secured control once more, and he seldom falls farther than his fetlocks.

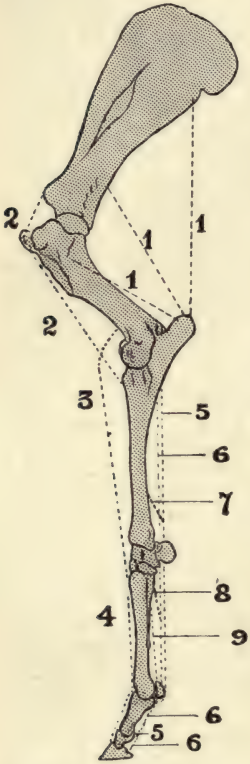


Fig. 185.—Bones of the Fore-Leg of the Horse, in the Attitude of Standing.

The dotted lines show the principal mechanism by which the limb is kept rigid.

1, 1, 1, The great triceps muscle; 2, the flexor of the arm; before insertion it gives off a slip of tendon to the extensor of the metacarpus, 3; 4, the extensor tendon of the foot; 5 and 6, the flexors of the foot; 7 and 8, the check ligaments; 9, the suspensory ligament.

It seems quite legitimate to regard the muscular union between the thorax and the fore-limb as a joint. There are no bones resting on each other, no synovia; but where the scapula has its largest range of movement there is a remarkable amount of areolar tissue, which renders movement easy. The whole central area beneath the scapula and humerus not occupied by muscular attachment, is filled with this easy-moving, apparently gaseously distended, crepitant, areolar tissue, over which the fore-legs glide on the chest wall as freely as if the parts were a large, well-lubricated joint. The animal's body is slung between the fore-legs, and the muscle principally, if not wholly, engaged in this important function is the thoracic portion of the *serratus magnus*. The tendinous cover to this immense muscular plate imparts additional strength, and is present in all muscles where strain is constant or long continued (see p. 391). The serratus magnus, on contracting, also draws the posterior and upper part of the scapula downwards; this is antagonised by its cervical portion. This muscle is a good example of a single muscle being so arranged in its fibres that they may act together or in opposition. During the standing attitude the fibres of this muscle are acting together, but in opposite directions, in order to maintain the scapula in a fixed position. During locomotion the portions are acting alternately (see Fig. 188).

The fixation of the scapula is the first essential step towards a standing attitude, and it is secured by the *serratus magnus*, *rhomboideus*, and *trapezius* (see Figs. 187, 188). The humerus below has now a firm bed to press against, as the scapulæ are prevented from being driven through the withers by the serratus. It is essential for the humerus that the shoulder-joint should be fixed and the elbow-joint locked. The large muscular mass of the triceps, acting from the humerus and scapula on the ulna, is mainly engaged in effecting this (Fig. 185, *1*). The more powerfully the triceps contracts, the more firmly is the beak of the ulna forced into the olecranon fossa of the humerus. It is this mechanism which keeps the elbow-joint locked. But, bearing in mind what has previously been said about the absence of exclusiveness in muscles, it is evident that the flexors of the fore-leg act passively on the elbow and keep it firmly extended (Figs 185, *5* and *6*), while the *biceps brachii* (*flexor brachii*), through its connection with the main extensor muscle of the limb, helps to keep the scapula in position and the shoulder-joint from opening in front (Fig. 185, *3*). This is a good example of co-operative antagonism. Here we see the flexor of the arm, extensor of the leg, and extensor of the elbow, all of which are antagonists when actively contracting, working together with one common object in view. The tendon running throughout the length of the biceps is of invaluable assistance in keeping the shoulder-joint fixed while the limb is in the standing position ; it acts, in fact, as a ligament from scapula to radius (Fig. 185, *2*).

The shoulder and elbow being fixed, the next joint, the knee, is far more easily controlled. From the knee to the foot it is only necessary to prevent the joints opening in front in order to maintain the limb rigid and upright, and to ensure this each segment of the limb is furnished with an extensor tendon (Fig. 186). There is a large one to the knee, and another to the pastern and foot, both of which are in turn reinforced for extra strength. The muscles which manipulate this locking apparatus run from the humerus, cross the front of the elbow-joint, and are distributed segment by segment until the foot is reached. Their efficacy in locking the fore-limb from the elbow to the foot depends upon the elbow-joint itself being firmly extended and locked. The large knee extensor receives powerful assistance from the *biceps brachii* in the form of a ligament which runs from the biceps to the extensor (Fig. 185, where *2* and *3* meet).

The position thus created is as follows : The biceps during the standing attitude, though not out of action, is not engaged in flexing the elbow. It is a flexor muscle which, we have just seen, is passively resisting the triceps, but it does not hesitate to help an extensor, an opponent, during the time it is not otherwise actively employed on its own special duty. This is a good example of the non-party feeling shown by muscles, and their desire for general rather than special utility.

The weight from the elbow to the foot is carried on the flexor muscles of the arm, of which there are five, three not proceeding below the knee, to the back of which they obtain attachment, and two which run the entire length from elbow to phalanges.

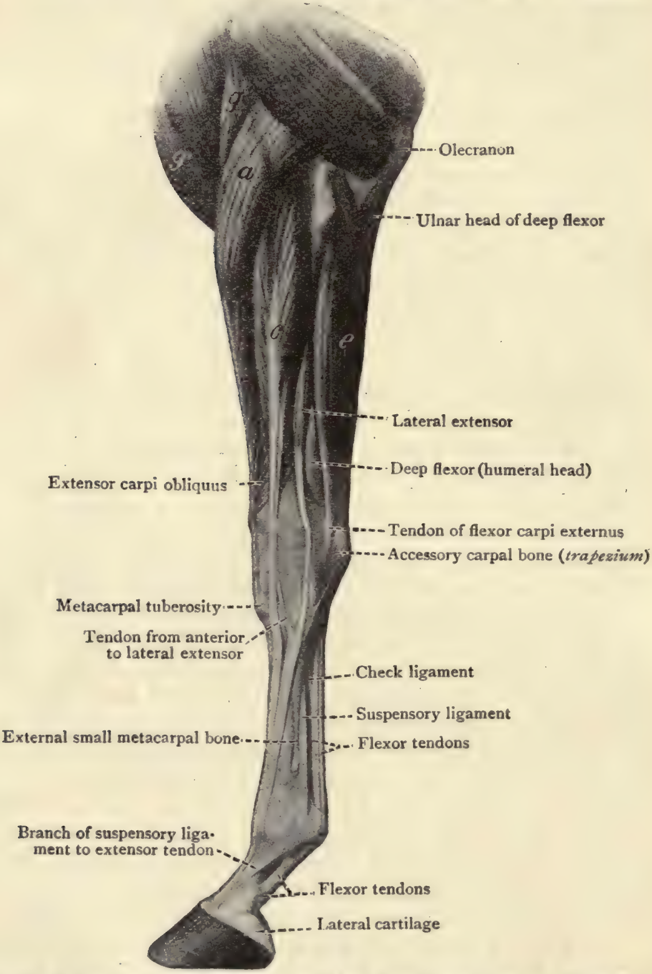

g'
g
a
Olecranon
Ulnar head of deep flexor
c
e
Lateral extensor
Deep flexor (humeral head)
Extensor carpi obliquus
Tendon of flexor carpi externus
Accessory carpal bone (*trapezium*)
Metacarpal tuberosity
Tendon from anterior to lateral extensor
Check ligament
Suspensory ligament
External small metacarpal bone
Flexor tendons
Branch of suspensory ligament to extensor tendon
Flexor tendons
Lateral cartilage

FIG. 186.—MUSCLES OF OUTSIDE OF NEAR FORE-LIMB OF THE HORSE (ELLENBERGER-BAUM-SISSON).

a, Extensor carpi radialis ; g, brachialis ; g', anterior superficial pectoral ; c, anterior or common digital extensor (extensor pedis) ; e, flexor carpi externus.

All these flexor muscles are characterised by the presence in their substance of a considerable amount of fibrous tissue, and both at the knee and elbow are fused with the fascia of the fore-arm, by which means additional support under continuous strain is obtained. But it is by the two long flexors, the *superficial* and *deep digital* (*flexor perforatus* and *perforans*) (Figs. 185, *5*, *6*; and 186), that the main support to the bony column is given, and this is obtained through the limb bending forward at the fetlock and these two tendons passing beneath and supporting the bent joint. The weight of the body presses the fetlock to the ground. The counteracting force of the flexor tendons sustains that weight, and maintains the fetlock in position. They are not the only mechanism supporting the fetlock, for there is the suspensory ligament, of which later; but the flexors are the chief support and, if divided, the fetlock sinks appreciably closer to the ground. The changes occurring in the fetlock-joint when an animal from injury or other cause is compelled for some time to support its body weight entirely on one limb throw light on the mechanism of the joint. It is not the muscular portion of the supporting flexors which gives way under the strain, but the tendinous portion, and this is well seen at the fetlock-joint. The bursa of the tendons at the part is dry; the tendons are dry, yellow, and shrunk. The interior of the fetlock-joint reveals nutritive changes, brought about by long-continued compression. The articular cartilage has become so thin that the bone has the barest possible covering, the joint is dry and yellow, and so intense has been the pressure that the actual pattern of one joint surface may be imprinted deeply on its fellow, and this imprint is made on the posterior part of the articulation, and not on the anterior; in other words, the pressure falls behind.

The two long flexors running from elbow to foot are assisted in their duty as weight-bearers by means of so-called **check ligaments** (Figs. 185, 7, *8*; 186). These ligaments are running, not from bone to bone, but from bone to tendon, and make a tendon function as a ligament by cutting off, as it were, the muscular attachment beyond. The perforatus above the knee and the perforans below it both receive a check ligament, which under the long-continued strain of support enables the flexor muscles to relax and obtain a much-needed rest.

The mechanisms below the fetlocks are a continuation of those above it, the same extensor and flexor tendons being employed from elbow-joint to foot. The slope of the pastern is maintained by the flexors of the leg, and though a joint exists between the second and third phalangeal bone, its function, when the limb is in the standing attitude, is not in evidence. In looking at the slope of the pastern, the eye always regards it as one bone, instead of two. The reason is obvious. There is very little movement in the joint between the corona and suffraginis at any time, and there is still less when standing. They are united by a dense

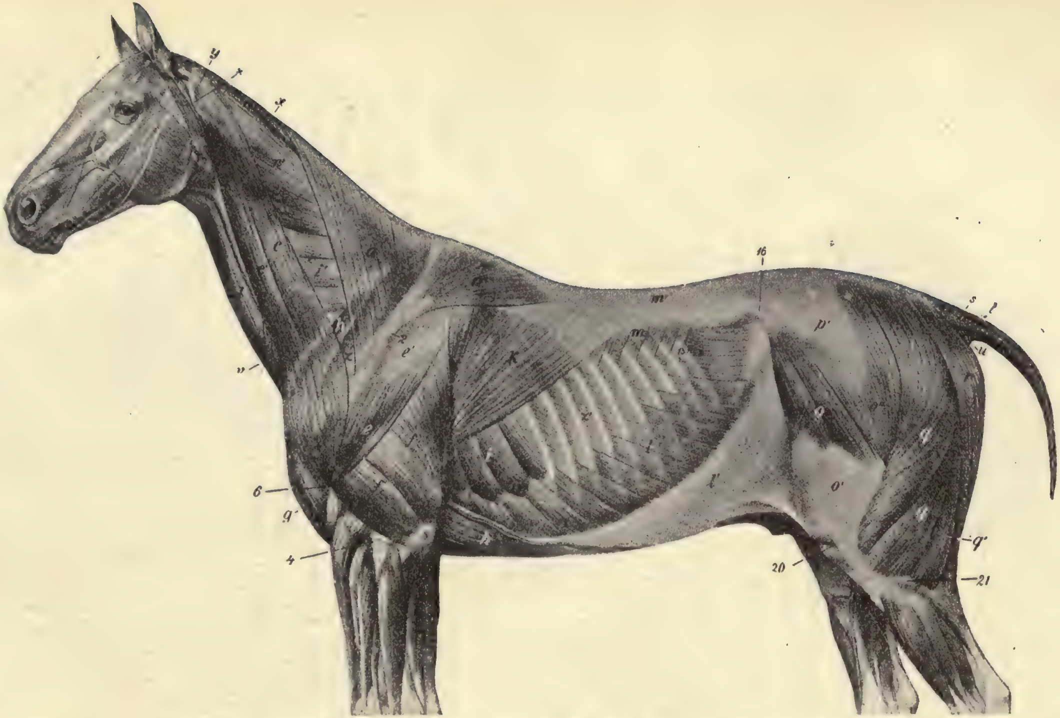


FIG. 187.—SUPERFICIAL MUSCLES OF THE HORSE (ELLENBERGER-BAUM-SISSON).

The panniculus, excepting the cervical part, has been removed. *a*, *Cervical trapezius*; *a'*, *thoracic trapezius*; *c*, *c'*, *mastoido-humeralis* (*levator-humeri*); *d*, *sterno-cephalicus*; *e*, *deltoid*; *f*, long head of *triceps*; *f'*, external head of *triceps*; *g*, anterior superficial *pectoral*; *h*, posterior deep *pectoral*; *h'*, anterior deep *pectoral*; *i*, *thoracic serratus*; *i'*, *cervical serratus* (*serratus magnus*); *k*, *latissimus dorsi*; *l*, *oblique abdominis externus*; *l'*, aponeurosis of *l*; *m*, *serratus posticus*; *m'*, lumbo-dorsal fascia; *o*, *tensor fasciæ latæ*; *o'*, *fascia lata*; *o''*, superficial *gluteus*; *q*, *q'*, *q''*, *biceps femoris*; *r*, *semitendinosus*; *s*, *t*, *u*, muscles of tail; *v*, *cervical panniculus*; *w*, *splenius*; *x*, *rhomboideus*; *y*, tendon of *trachelo-mastoideus* and *mastoido-humeralis*; *z*, *supra-spinatus*; *x*, wing of atlas; 2, spine of scapula; 4', external epicondyle

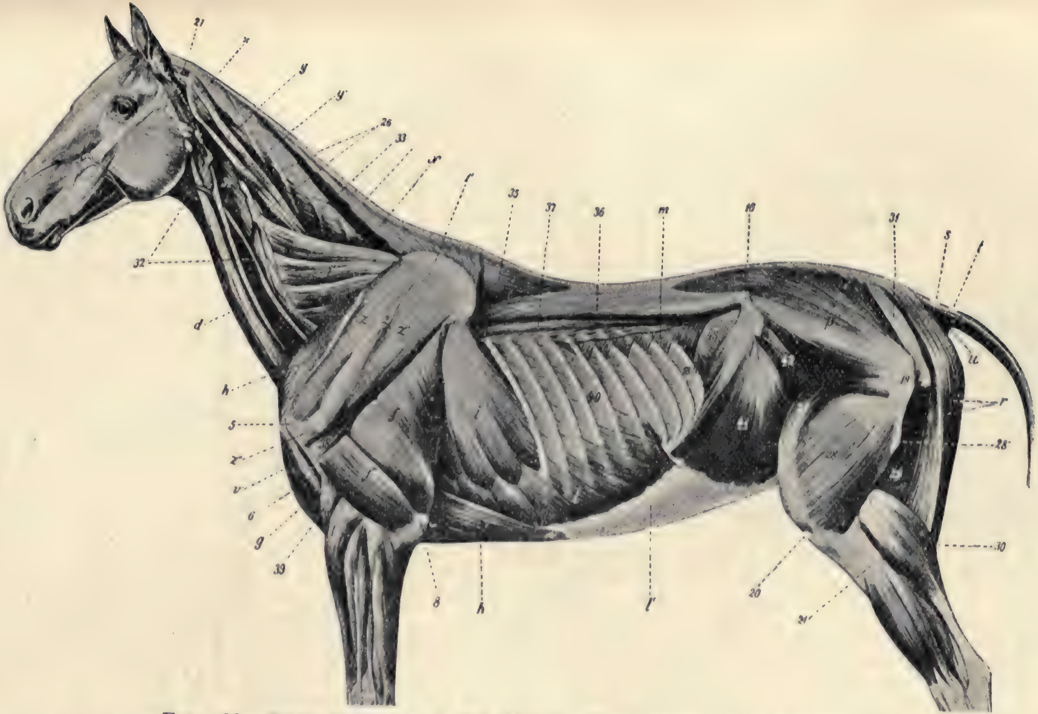


FIG. 188.—DEEP MUSCLES OF THE HORSE (ELLENBERGER-BAUM-SISSON).

Long head of *triceps; f′*, external head of *triceps*; *g*, anterior superficial *pectoral*; *h*, posterior deep *pectoral*; *h′*, anterior deep *pectoral*; *i*, *thoracic serratus*; *i′*, *cervical* serratus; *l*, *oblique abdominis externus*, and *l′*, its aponeurosis, the posterior part of which has been removed; *m*, *serratus posticus*; *p*, *gluteus medius*; *r*, *semitendinosus*; *s*, *t*, muscles of tail; *v′*, *biceps brachii*; *x*, *rhomboideus*; *y*, *y′*, *trachelo-mastoideus*; *z*, *supra-spinatus*; *z′*, *infra-spinatus*; 1, cartilage of scapula; 2, spine of scapula; 5, external tuberosity of humerus; 6, deltoid tuberosity; 8, olecranon; 16, external angle of ilium; 19, trochanter major; 20, patella; 21′, external condyle of tibia; 26, articular processes of cervical vertebræ; 28, *vastus internus*; 28′, *rectus femoris*; 28″, trochanter tertius; 29, *semimembranosus*; 30, *gastrocnemius*; 31, sacro-sciatic ligament; 33, *complexus*; 34, *rectus capitis anterior major*; 35, *spinalis dorsi*; 36, *longissimus dorsi*; 37, *transversalis costarum*; 38, *teres minor*; 39, *brachialis*; 40, external *intercostal*; 41, *oblique abdominis internus*; 42, *iliacus*; 43, *transversalis abdominis*.

feltwork of ligamentous material, and, as we shall see later in studying the limb in movement, the chief motion occurring in the pastern bones is between the corona and pedis.

The fore-limb is kept vertical and the pastern bent by the insertion of the perforans tendon into the pedal bone ; every joint from the elbow to the foot is locked by its extensor tendons and supported by its flexors, the fascia of the arm binding up and supporting both groups.

In the hind-limbs the standing attitude is simpler, owing to the existence of the **hip-joints** beneath the horizontal spine. The attitude assumed by the legs is the result of flexion in some joints, extension in others. The hip-joint is flexed by the *psoas magnus*, *iliacus*, *tensor fasciæ latæ*, *gluteus superficialis* (*gluteus externus*), and *pectineus* muscles. Considering the enormous amount of muscular tissue belonging to the hind-quarters, it is rather remarkable that so little of it is required for hip-flexion, for the above, relatively speaking, are not bulky muscles. The extensors of the hip-joint, on the other hand, are very large—*i.e.*, the insertions of the large *biceps femoris*, *gluteus medius*, and *semimembranosus* (see Figs. 187 and 188).

The above groups of muscles fix the head of the femur rigidly so far as to-and-fro and outward movements are concerned, but the joint has also to be supplied with support on its inner side, and this is effected by the *great* and *small adductors* and *gracilis*. The resultant of the pull of these muscles on the hip-joint is the position assumed by the femur in standing, and the angle it forms with the pelvis depends upon whether the limb is bearing weight or resting. The joint below the hip is the *stifle*, and the part this plays in attitude is considerable, for no flexion of the hind-leg can possibly take place without the concurrence of the stifle. The stifle is flexed by means of the *biceps femoris*, *semitendinosus*, and *gracilis* (Figs. 187, 189) ; it is extended by the *rectus femoris* and *vasti* muscles (Fig. 188). Unless these latter concur, flexion of the stifle is impossible. So slight, indeed, is the effort required to keep the stifle rigidly extended that if *one* hand grasps the muscles inserted into the patella, and presses the bone back on the femur—the horse having just been destroyed —no ordinary force employed at the foot-end of the limb can flex the hock, and the hock cannot flex without the stifle flexing.

Tendo-Ligaments of the Thigh.—From the above it is evident that very little muscular effort is required to keep the largest joint in the body fixed during the standing attitude. In addition to the muscles inserted into the patella, the stifle is also kept extended by the contraction of the *anterior digital extensor* (*extensor pedis*), *peroneus tertius*, and *tibialis anticus* (*flexor metatarsi* muscular and tendinous division)—a pair of muscles (Fig. 190)

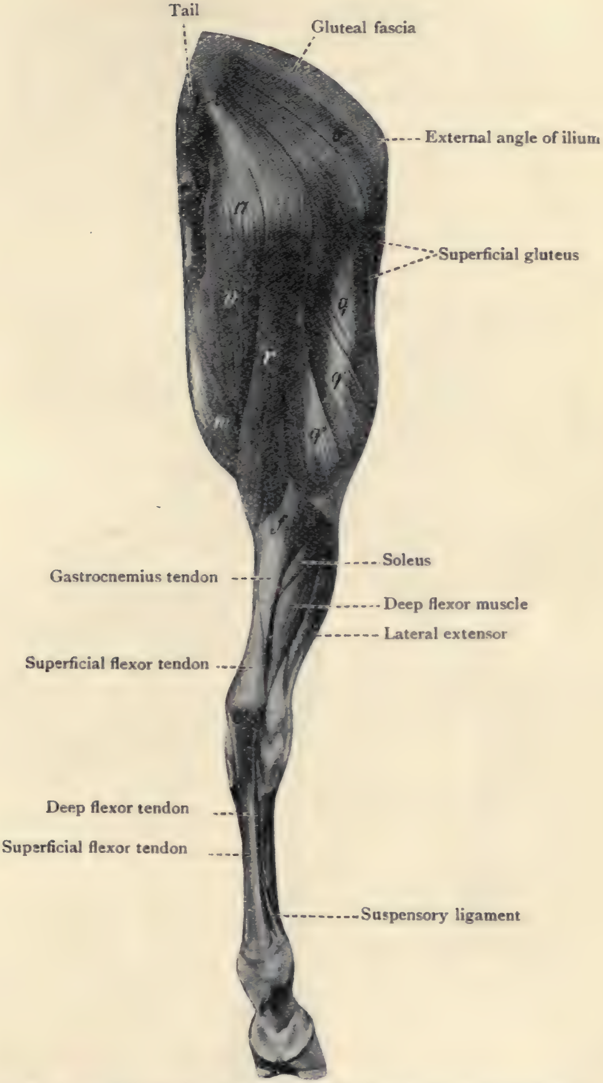

Tail
Gluteal fascia
External angle of ilium
Superficial gluteus
17
v
q
r
q'
w
q"
f
Soleus
Gastrocnemius tendon
Deep flexor muscle
Lateral extensor
Superficial flexor tendon
Deep flexor tendon
Superficial flexor tendon
Suspensory ligament

FIG. 189.—MUSCLES OF OFF HIND-LIMB OF HORSE (ELLENBERGER-BAUM-SISSON).

17, Position of *tuber ischii* ; o", superficial *gluteus*; *q, q', q", biceps femoris* ; *r, semitendinosus* ; *v, semimembranosus* ; *w, gracilis* ; *f, gastrocnemius.*

attached to the external condyle of the femur by means of a common tendon. The tendon runs from the stifle to the hock-joint, and is a cord of great strength, acting not only as a tendon to the muscles which envelop it, but also as a long straight ligament (Fig. 191, *3*). Chauveau describes the action of this tendo-ligament as possessing the property of flexing the hock automatically in conformity with flexion of the stifle. but he also regards its other use as that of keeping the stifle-joint extended. It is impossible for the flexor metatarsi to act while the stifle is kept locked, and there can be no doubt that the action of the cord as a long ligament is of great value in relieving

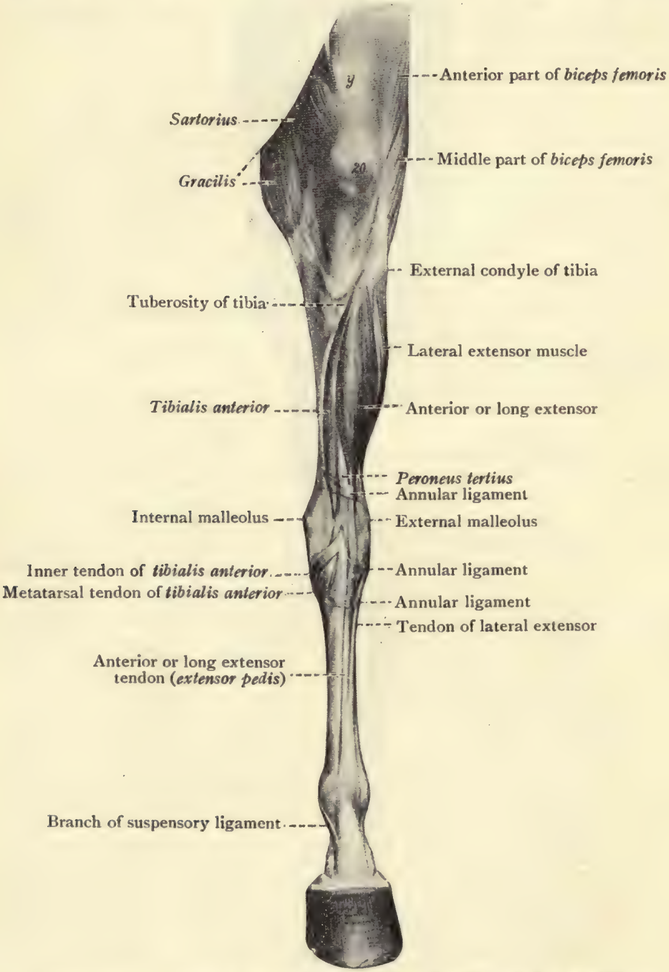
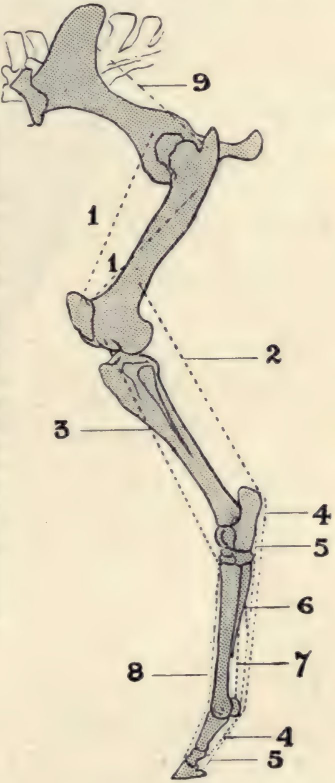

y
Anterior part of *biceps femoris*
Sartorius
20
Middle part of *biceps femoris*
Gracilis
External condyle of tibia
Tuberosity of tibia
Lateral extensor muscle
Tibialis anterior
Anterior or long extensor
Peroneus tertius
Annular ligament
Internal malleolus
External malleolus
Inner tendon of *tibialis anterior*
Annular ligament
Metatarsal tendon of *tibialis anterior*
Annular ligament
Tendon of lateral extensor
Anterior or long extensor tendon (*extensor pedis*)
Branch of suspensory ligament

FIG. 190.—MUSCLES OF NEAR HIND-LIMB OF HORSE, ANTERIOR VIEW (ELLENBERGER-BAUM-SISSON).

y, *Rectus femoris* ; *20*, patella.

the strain from the flexor metatarsi muscle. That the cord is not absolutely essential to standing may be determined experimentally by dividing it, or clinically by the rupture which occasionally occurs. It is the antagonist of a similar tendo-ligament at the back of the tibia, which runs from the femur to the calcis, the function of which is to oppose hock-flexion (see Fig. 191, *2*).



The dotted lines indicate the powerful mechanism for maintaining the limb in a rigid condition. 1, 1, The muscles which keep the patella drawn up and the stifle-joint locked; 3, the flexor of the hock and metatarsus automatically affected by 1; 2, The *gastrocnemius* and *flexor perforatus* muscles, both keeping the hock extended in opposition to 3. In 2 and 3 tendinous cords run from end to end, and so act as ligaments, keeping the parts in the relation prescribed by the patella without great muscular effort. 4, The perforatus below the hock; 5, the perforans; 6, the check ligament; 7, the suspensory ligament; 8, the extensor of the foot; 9, the *gluteus maximus* keeping the hip-joint extended.

Fig. 191.—Bones of the Hind-Leg of the Horse in the Attitude of Standing.

The Hock.—The muscles which keep the hock extended (Figs. 191, *2*; 192) are—(1) The *gastrocnemius*, running from the femur to the calcis, to which it is attached. It is an active extensor when the foot is off the ground, a passive extensor when the weight is resting on the limb. (2) The *superficial digital flexor* (*flexor perforatus*), which runs from the femur to the calcis, to which it is attached, forming a tendinous cup into which the point of the calcis fits, and subsequently running down the back of the limb to be inserted into the second phalanx. This muscle is almost entirely tendinous. It is the tendo-ligament (Fig. 191, *2*) antagonistic to the flexor metatarsi (Fig. 191, *3*) previously described. During the attitude of standing it relieves the constant strain which would otherwise be imposed on the gastrocnemius, and maintains the hock extended. It is not only an extensor of the hock, but one of the flexors of the lower limb.

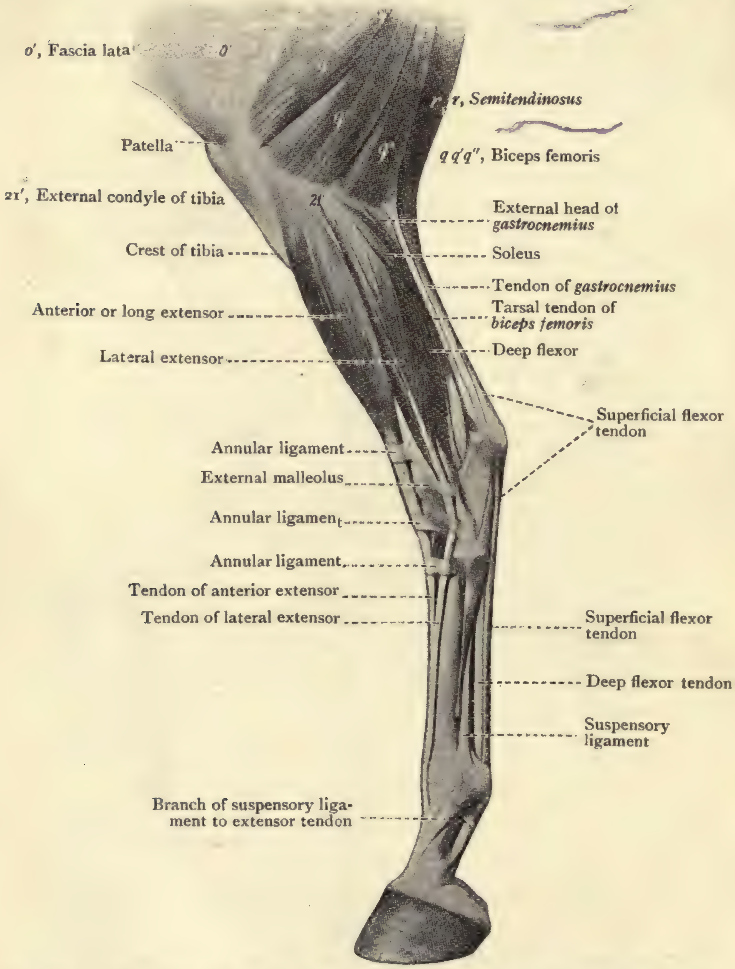

o′, Fascia lata
o′
r, *Semitendinosus*
Patella
q q′q″, Biceps femoris
21′, External condyle of tibia
21′
External head of *gastrocnemius*
Crest of tibia
Soleus
Tendon of *gastrocnemius*
Anterior or long extensor
Tarsal tendon of *biceps femoris*
Lateral extensor
Deep flexor
Superficial flexor tendon
Annular ligament
External malleolus
Annular ligament
Annular ligament
Tendon of anterior extensor
Tendon of lateral extensor
Superficial flexor tendon
Deep flexor tendon
Suspensory ligament
Branch of suspensory ligament to extensor tendon

FIG. 192.—MUSCLES OF LOWER PART OF THIGH, LEG, AND FOOT OF HORSE, EXTERNAL VIEW (ELLENBERGER-BAUM-SISSON).

The Reciprocating Action of Stifle and Hock.—From what has been said, it is evident that flexion and extension of stifle and hock are identical in their action. When the stifle is extended, the hock is automatically extended, nor can it under any circumstances flex without the previous flexion of the stifle. There is no parallel to this in the body. The two joints, though far apart, act as one, and they are locked by the drawing up of the patella, and in no other way (Fig. 191, *1*). The so-called *dislocation of the stifle* in the horse is a misnomer. That the patella is capable of being dislocated is beyond doubt, but the ordinary condition described under that term, when the stifle and hock are rigid while the foot is turned back with its wall on the ground, is nothing more than spasm of the muscles which keep the patella drawn up (Fig. 191, *1 1*). The moment they relax the previously immovable limb and useless foot have their function restored as if by magic, but are immediately thrown out of gear in the course of a few minutes as a recurrence of the tetanus of the patellar muscles takes place. The fascia of the thigh, like that of the arm, is a most potent factor in giving assistance to the constant strain imposed on the muscles of the limbs during standing.

Below the hock the hind-limb is arranged like that of the fore, the deep flexor (*perforans*) receiving its additional support from the 'check ligament,' as in the fore-leg (Fig. 191, *6*).

The natural **attitude of standing** adopted by the horse is to rest on three legs—one hind and both fore. If he is alert, he stands on all four limbs; but if standing in the ordinary manner, he always rests one hind-leg. He does not remain long in this position without changing to the other. Hour by hour he stands, shifting his weight at intervals from one to the other hind-leg, and resting its fellow by flexing the hock and standing on the toe. He never spares his fore-limbs in this manner in a state of health, but always stands squarely on them. The moment he places one fore-foot in advance of its fellow—'pointing,' as it is termed—the experienced eye knows that something is wrong. Many years ago the writer suggested that the periodical resting of the hind-feet was the possible explanation of their freedom from navicular disease. The horse only rests the fore-feet when they are already subjects of this disorder.

Distribution of the Weight on the Limbs.—The fact that the animal rests the hind-limbs, and never the fore, suggests that the weight carried by the former is greater than that carried by the latter. The reverse, however, is the case. The fore-legs carry from 9 to 19 per cent. more weight than the hind. The weight on the fore-limbs is increased when the head is depressed, and reduced when it is raised. The latter movement displaces the centre of gravity backwards, and throws more weight on the hind-limbs, for the head of the horse is very heavy, being from 40 to 50 pounds in weight, more or less, depending on size and breed.

The Centre of Gravity.—During the standing attitude this lies near to the intersection of a horizontal line, below the shoulder-joint and a vertical line passing about 6 inches behind the elbow. During locomotion, jumping, draught, etc., the position is constantly shifting from front to rear and from side to side, depending on the position of the body and the pace.

Lying Down.—The attitude assumed by a horse in lying down is quite characteristic. He has only two positions—one flat on his side, with the legs and head fully extended, and the other with the head and spine raised, sitting obliquely on his chest. He cannot sit directly on the sternum, owing to its sharp edge, so the body inclines to one side in order to avoid it. In this attitude of repose both knees and hocks are bent, all four feet are brought under the body and arranged on one plan, which is never departed from. If, for instance, he is sitting on his chest inclined to the near side, the near fore-foot is placed close to the breast-bone, the elbow touching the ground—in fact, the body is resting largely on the near elbow. The near hind-foot is under the abdomen, the outer part of this limb, both hock and shank, resting on the ground. The off fore-foot lies close to its elbow, but outside it. The elbow does not rest on the heel of this foot, as is so frequently taught, and consequently never suffers injury from the heel of the shoe. The off hind-foot is flexed and brought forward towards the elbow, while the point of the hock of this limb rests on the ground. A ' capped elbow ' never occurs from the heel of the shoe, but is due to the underneath elbow coming in contact with the ground. Similarly, a capped hock may be aggravated or originate from resting on the point of the hock when lying. The horse, as a rule, sleeps fully extended on his side, but, should he sleep in the chest position, he rests the chin on the ground, often everting the lower lip, so that the teeth take the pressure. Cattle and sheep repose on the chest. The flat sternum is perfectly adapted to this, the only position normally adopted. During sleep they turn the head round to one side, the nose being placed towards the flank.

The Act of Rising is only performed in one way by horses and cattle, and in each animal the method is reversed. No horse can rise until he has placed his fore-legs out in front. The first effort made is to unbend each knee alternately, and get the feet out in front, resting on the heels. The hind-legs are well flexed, the feet placed under the centre of the belly, and the animal reaches the standing position by means of the hind-legs, with the aid of the fore. The body follows the head, and if the head be kept down no horse can rise. All ruminants rise tail foremost. Resting on both knees, they raise the hind-quarters, straighten the limbs, and then rise in front.

Joints.—Before examining the second function of muscles—viz., the production of locomotion—it is necessary to look again at the question of joints. These have been studied in connection with their static function; they must now be looked at from their kinetic aspect.

Whenever two bones come together a joint is formed and arrangement provided against the production of friction. Whenever any two surfaces meet, one of which is moving on the other—such as tendons passing through grooves or working over bony projections—similar anti-friction appliances exist. We have even ventured to regard the adjustment of the fore-leg on the chest wall as a joint, although wholly muscular, and have pointed out (p. 590) in what way friction is provided against. It has been shown that the joints of the limbs of the horse are furnished with automatic appliances for maintaining position with the least muscular effort, and enabling the animal to stand continuously for long periods. The features now to be considered are those connected with the movements of joints.

The **Shoulder-Joint** is remarkable for the small surface afforded by the scapula, and the large area existing on the humerus. This allows great freedom of movement in both a to-and-fro and side-to-side direction. There is no bone in the body the movements of which resemble the scapula, and there is no joint which resembles that formed by it with the humerus. There are no separate ligaments to the joint; the tendinous insertions of the muscles are the ligaments, and this provision would appear to be associated with the immense freedom required in the rolling action of one bone on the other. Both in the fore and hind limbs the two upper bones of the leg are arranged to form an obtuse angle, and this is peculiar to quadrupeds. In the biped the humerus is not bent from the vertical, nor are the femur and tibia. The object of the bending is to ensure great rapidity of action and destroy concussion; there is far less jar in dropping on a limb in which the column of bones is bent towards each other than in a column which is vertical. The scapula and humerus form an angle of about 120 degrees. The shoulder-joint is lifted—viz., the fore-limb is advanced—by only one muscle, the *mastoido-humeralis* (*levator humeri*) (Fig. 187). Arising from as high as the head and atlas, this immense muscle is solely responsible for advancing the limb. The numerous and complex movements occurring throughout the whole length of the leg on the shoulder being raised may here be outlined. The shoulder cannot be advanced with the foot on the ground, so the weight must first be transferred to its fellow; the elbow-joint is next unlocked by a relaxation of the extensor muscles, which are inserted into the ulna; the *biceps brachii* (*flexor brachii*) next contracts to carry the arm forward, and by so doing assists to flex the elbow,* the flexor muscles of the back of the limb contract in order to flex the foot and all the joints as high as the knee. The column of bones being broken as described and the whole limb made flexible, it is carried forward, the thoracic portion of the *serratus magnus* and *trapezius* pulling one angle of the scapula backwards, and the *latissimus dorsi* flexing the humerus on the scapula. The limb having been advanced sufficiently, the flexible column of bones is once more made rigid. First the

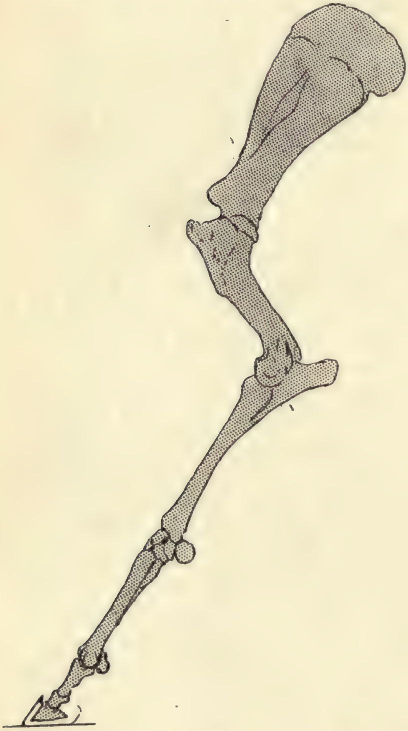


Fig. 193.—The Position of the Column of Bones of the Fore-Leg when the Foot makes Contact with the Ground.

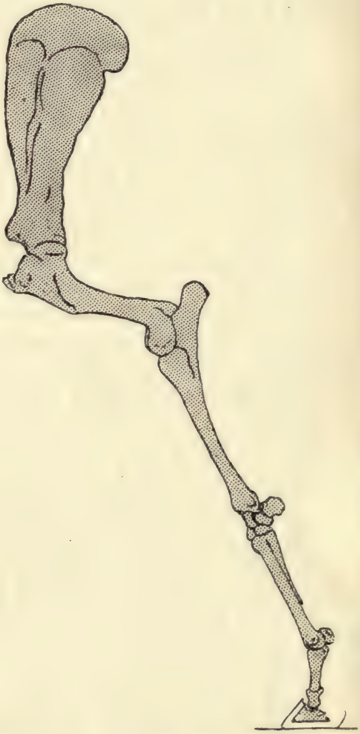


Fig. 194.—The Position of the Column of Bones of the Fore-Leg preparatory to Final Propulsion.

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* At this moment it is lifting a weight of about 17½ pounds (8 kilos) in a riding-horse, this being the weight of the limb from elbow to foot, exclusive of the shoe.

extensors of the carpus and foot act, straighten the limb at the knee, and put the foot in position to receive the weight of the body when it comes to the ground. The effort to advance the leg is trifling, and the foot having made contact, the limb being in the position shown (Fig. 193), the real work now begins, for the body has to pass over the limb, while the leg remains fixed and rigid from elbow to foot. The muscles which pull it over are the *latissimus dorsi* acting on the humerus, and the large *deep pectoral* muscle (see Fig. 188), which, running forward from the ninth or tenth ribs and sternum beneath the fore-leg, to the shoulder-joint, pulls the whole shoulder-joint backwards, and causes the body to rotate over the limb. It is powerfully assisted in this by the *cervical serratus* and *trapezius* drawing the scapula forwards and upwards, and the large head of the *triceps* pulling on the ulna. At the end of the movement the column of bones is in the position shown in Fig. 194, and the final act of the limb is about to occur—viz., its propulsive motion. To effect propulsion, the limb remains rigid while the long flexors of the arm straighten the pastern, until little more than the toe of the foot is on the ground; then, with a sudden sharp contraction of these muscles, the body is propelled upwards and forwards, the limb being flexed (Fig. 195), carried to the front, unbent, and again placed on the ground.

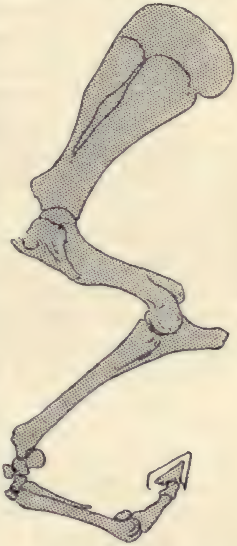

FIG. 195.—THE COLUMN OF BONES FORMING THE FORE-LEG BROKEN UP, THE LIMB SHORTENED BY FLEXION AT SHOULDER, ELBOW, KNEE, FETLOCK, AND BEING CARRIED FORWARDS.

The **Elbow-Joint** has already occupied attention, more particularly in connection with its locking during the attitude of standing. During locomotion extensive hinge-like motion occurs, which is abnormally exaggerated in high-steppers. The hinge has two condyles and a ridge on the humerus, which fit into a reverse moulding on the radius. The internal condyle is much the larger, and occupies about half the entire articular surface. These condyles, during flexion of the joint, turn the knees outwards. If they throw them out too far, the leg below the knee is thrown in, and so causes "brushing" and "speedy cutting." This movement is best seen from above when mounted; Though a hinge-joint, the arm appears to describe a semicircle in the sweep it makes on flexion of the elbow. It is greatly exaggerated in some horses.

The **Knee-Joint** consists of three main joints and numerous minor ones. The articulatory surface of the radius with the upper row of knee-bones has no parallel in the body; it is a surface both deeply concave and markedly convexo-concave. The concavity and convexity on the radius form condyles of which the inner is more curved than the outer. The concavity on the anterior part of the radiocarpal articulation rests on the convex surface of the upper row of knee-bones, and in this way a firmer and closer union between these surfaces is obtained, such as is needed in the upright condition of the limb. But when this joint is flexed, the convex posterior surface of the radius comes forward; this depresses the *scaphoid* (*radiocarpal*), and produces between it and the *semilunar* (*intermediate carpal*) a very important movement by which the foot is thrown slightly outwards, probably with the object of enabling it to clear the opposite limb. The upper joint of the knee possesses the largest range of motion, the middle joint very much less, the lower joint hardly doing more than gliding on its fellow. Percivall pointed out many years ago that the *trapezoid* rests wholly on the head of the inner splint bone, which explains the frequency with which this bone becomes affected with 'splint.'

The **Fetlock-Joint** forms a special variety of articulation, one which is firm and rigid anteriorly, elastic and yielding posteriorly. This is effected by introducing two sesamoid bones into the fetlock articulation, and suspending them between ligaments: the structure by means of which the sesamoids are suspended is the **Suspensory Ligament** (Fig. 186). This runs from the back of the large metacarpal bone to the fetlock, receiving insertion into the sesamoids. The latter are floating bones, and, speaking more generally, perhaps, than an anatomist would admit, they are embedded in ligamentous material which keeps them in their place. The suspensory ligament supports them above and laterally; the sesamoidal ligaments keep them fixed below. The anterior face of these bones forms the posterior face of the fetlock-joint.

There is no other joint in the body the mechanism of which has received so much attention as that of the fetlock and suspensory ligament. The rival theories have been divided on the question of the elasticity of the suspensory ligament. Gamgee (senior) regarded it as absolutely non-elastic; he did not believe that it supported the sesamoids, but regarded it as acting powerfully in flexing the foot, being brought into action or set free according to the position of the limb. It was he who destroyed the notion once and for all that the sesamoids moved up and down.

The fetlock-joint furnishes the only example in the body of a bone placed vertically resting on one placed obliquely. The metacarpal rests on an inclined plane in the form of the suffraginis, and but for the sesamoids would slip off at the back. It is one of the functions of the sesamoids and suspensory ligament to keep this bone in its place, and so support the fetlock under stress.

The sesamoid bones are also intended to furnish the fetlock-joint with a yielding articulation, which receives the weight of the body when the foot comes in contact with the ground. At the moment this occurs the whole pastern from fetlock to foot becomes more oblique, giving the appearance of sinking, which in reality occurs. The sinking, however, is not due to displacement of the sesamoids, but to increased obliquity of the pastern under stress, owing to which the suspensory ligament is under great strain. It does not appear to be reasonable to deny it some degree of elasticity—viz., the power to stretch slightly and then return to its original length ; but the stretching is not great, and can be reproduced on a limited scale by lifting up the opposite fore-leg, and observing the tense, sharp lines produced in the suspensory at the moment the fetlock descends, through increased obliquity of the pastern. The evidence that the suspensory supports the fetlock is shown by the effect of dividing it, which brings the fetlock appreciably nearer to the ground, while the evidence that the suspensory ligament only possesses limited elasticity is furnished clinically by the frequency with which it is sprained. If it were highly elastic, a sprain would be a difficult matter. No one, for instance, ever heard of the only elastic ligament in the body being sprained—*i.e.*, the *ligamentum nuchæ*—but a ligament of this nature in any part of the limbs would be useless. If tendons and ligaments were highly elastic, the efficient action of muscles would be destroyed, for during contraction their tendons would be stretching instead of pulling.

It is quite easy to show that in the ordinary standing attitude the sesamoid bones, together with the posterior half of the metacarpal articulation, bear the weight of the body, while the anterior surface of the suffraginis and metacarpal takes but a small share. The two movements of the fetlock-joint are flexion and extension. Flexion in every other joint in the body but the fetlock begins by bending, but when the fetlock is flexed the pastern has first to become straight before it can be bent backwards. Flexion of this joint is accomplished by the *perforans* and *perforatus*, while extension is brought about by the *extensor* of the foot and *suffraginis*. The more the foot is extended, the greater the strain on the sesamoids, and the slip of the suspensory ligament which joins the extensor tendon (Fig. 186,) may at this time be associated with the action of this tendon, drawing the sesamoids closer to their articulating surface the more extended the fetlock becomes. Or the slip may be considered in the light of an extension of the suspensory ligament, in order to afford it increased surface of attachment. The use of the slip, however, is not very evident, and we have never seen it sprained, which is the best evidence that its share is not very important.

The suspensory ligament becomes sprained when the flexor muscles tire, for the fetlock-joint is supported not only by the suspensory ligament, but by both flexor tendons. Division of the *perforatus* produces very little effect on the dropping of the joint; division of the *perforans* creates evident effect, but it requires division of both flexors to bring the heel to the ground (see Fig. 196, *3*).

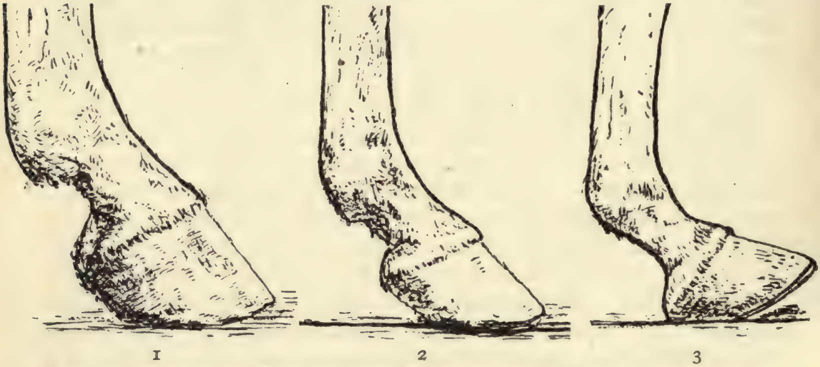

FIG. 196.—EFFECT OF EXPERIMENTAL DIVISION OF THE SUSPENSORY LIGAMENT AND FLEXOR TENDONS ON THE OBLIQUITY OF THE PASTERN (LISHMAN).*

1. Division of the suspensory ligament has caused the fetlock to drop a little.
2. Division of the *flexor perforatus* tendon has caused slight sinking of the fetlock.
3. Division of both *flexors*, *perforatus* and *perforans* tendons, brings the heel of the foot to the ground, and causes the toe to turn up.

The fetlock-joint does not come to the ground unless all the structures are divided.

Pastern-Joint.—This joint, formed between the first and second phalangeal bones, allows of limited flexion and extremely limited extension. It is, in fact, specially arranged to act during extension as if the first and second phalanx were only one bone, and that no joint existed between them. This function comes into play when the body rotates over the foot on the ground—*i.e.*, during the period the body is passing from the position in Fig. 194 to that in Fig. 195. When the limb passes the vertical, the two bones, owing to the arrangement of their ligamentous connections, move as one on the pedal articulation; in other words, the corona and suffraginis are immovably locked, and for the time being the joint between the fetlock and foot is obliterated. As the locking is entirely ligamentous, the strain must be considerable. When the foot comes to the ground, concussion to the pastern-joint is saved by the fibrous plate which exists at its posterior part. This plate is on the corona, and is hollowed out for the reception of the rounded surface of the suffraginis.

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* These figures are copied from photographs published in the *Veterinary Record*, August 22, 1908.

The Pedal-Joint is formed by three bones—the second and third phalangeal and the navicular bone. The chief movements occurring are flexion and extension. This joint is the centre of the entire movement of the leg; the body rotates over it. Relatively it is a small articulatory surface built up and strengthened by the hoof, the cartilages of the foot, the flexor and extensor tendons of the foot, and the connecting ligaments peculiar to the bones forming the joint. It is a yielding or elastic joint, due to the introduction of the navicular bone into its posterior part; this functions as a sesamoid, and by yielding under pressure counteracts shock. The pedal-joint is so deeply buried within the foot, and strengthened by the various structures named, that though it is the centre of movement during the passage of the body over the limb, it is practically immune against the diseases of locomotion, so common in other joints. Not so the joint last considered—the pastern; it is frequently the seat of trouble, probably due to the strain on the ligaments when the bones become locked during extension.

Joint-Locking.—Repeated attention has been drawn to joint-locking, and the example last given of the mechanism enables a more comprehensive statement to be made. The whole of the joints in the fore-leg of the horse are locked during extension, from knee to coronet. The only joints where movement is occurring are the shoulder, elbow, and foot (the articulation between the corona and pedis). The locking occurs when the limb on the ground is no longer vertical—when, in fact, it is assuming the position shown by the fore-leg in Fig. 193; from that moment every degree of further extension locks knee, fetlock, and pastern the tighter. This renders the limb from the arm to the foot as rigid as if it were composed of one piece of bone. It also explains why the posterior part of the knee-joint is one mass of interlacing ligamentous structure.

The Hip-Joint has a wide range of movement in the direction of flexion, extension, and rotation; but owing to the position of the *round ligament* (*ligamentum teres*), outward movement at right angles to the body is limited. The pubio-femoral ligament, which is confined to the horse, is derived from the prepubic tendon of the abdominal muscles. It is far from clear why a slip of tendon from the abdominal muscles should require to be inserted into the articulating head of the femur. During inward rotation of the thigh—as, for example, when the foot is on the ground and the body is passing over it—the pubio-femoral ligament is rendered tense (Sisson). When the ligament is long, the stifle turns outwards, the points of the hock turn in, and the condition known as 'cow-hocks' is produced. It will be observed that the production of cow-hocks has nothing to do with any part but the hip-joint. The insertion of the round ligament into the inner side of the head of the femur limits the outward movement of the limb, and is generally considered to explain why a horse so seldom 'cow kicks.'

The Stifle-Joint.—This is the largest joint in the body, and is built on quite different lines to any other. A large convex surface on the femur is placed resting on a flat surface on the tibia, with absolutely no bony cavity in which to rest or play. Shallow cavities are furnished by two plates of cartilage, which receive the condyles of the femur, and on which the latter rest quite superficially. It will be observed that, with this exception, no preparation exists on the tibia for the formation of this immense joint. Nothing could be more unlike in appearance than the in-contact ends of femur and tibia. The discs of cartilage, which take the place of bony cups, no doubt allow of considerable flexion and freedom of movement, but as a joint it is unreliable, and consequently the two bones are held together by two crucial ligaments running in opposite directions. These ligaments are somewhat twisted on each other, and when the joint is flexed the posterior ligament is rendered taut. Extension and flexion are the two principal movements of the stifle; during each of these the discs of cartilage on the tibia slide forward or backward on the bone in conformity with the movement of the femur, the movement of the external condyle and its cartilaginous cup being greater than that of the internal. The above is not the only joint formed by the stifle. In front is the patella, playing over two large convex surfaces, the trochleæ of the femur. The patella is a floating bone the same as the sesamoids; it appears to move up and down, but as it is attached below, this is impossible. It is the trochleæ of the femur which move, the large inner one doing the bulk of the work. The muscles inserted into the patella and the muscles which flex the hip-joint are direct antagonists. It is impossible for the hip or even so remote a joint as the hock, to flex so long as the patella muscles are maintained in a condition of contraction. When they relax, flexion of the hip-joint is permitted by means of the muscles already considered (p. 596); the tibia is drawn up by the *biceps femoris* and *semitendinosus* (Figs. 187, 189), the trochleæ of the femur appear above the patella, the *flexor metatarsi* is placed in operation and flexes the hock, and as the stifle becomes more and more flexed, the bulk of the whole joint increases, and is turned outwards from the abdomen, in order to accommodate its increase in size. This turning outwards of the stifle, a feature seen in any pace, but particularly well marked in the trotting horse, is not due to any mechanism in the stifle, but to the hock-joint. It will be shown presently that the ridges on the astragalus, through their action on the tibia, turn the stifle outwards.

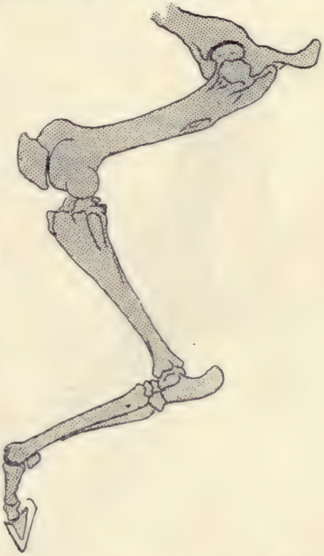

FIG. 197.—FLEXION OF THE HIND-LIMB.

The Hock-Joint is not only of physiological but of the greatest clinical interest, owing to its being the frequent seat of lameness. It is a hinge-joint, and a hinge in such a position on the limb must be of great strength to resist the tendency to close under the influence of the body weight. In fact, the hock-joint, unlike the knee, to which it corresponds, is under the constant stress of extension, which is the reason why, in spite of the automatic appliances with which it is furnished for keeping it open, the joint is always being alternately closed for the purpose of rest. The long lever at the back of the joint, in the form of the calcis, is a lever of the first order; it is the lever of power, and the strain on these muscles will be realised when it is remembered that the whole weight of the hind-quarters is supported by the *gastrocnemius* and *flexor perforatus* through their insertion into the calcis. The strain is largely removed by the introduction of a tendo-ligament—viz., a cord running from end to end within the muscle, and forming its two attachments, by which means it is capable of relieving much of the strain from the muscle. The existence of two such cords in the hock is described at p. 596 (see Fig. 191, *2*, *3*).

The two movements of the hock are flexion and extension; the extension, which occurs during the attitude of rest, is dealt with at p. 601. The extension of locomotion is carried on by the same mechanism—viz., the gastrocnemius muscle, and the tarsal tendon running from the biceps femoris muscle (*biceps* *abductor femoris*, or *long vastus*) to the calcis (see Fig. 192). It is seldom that the eye can witness *extreme* extension of the limb—*i.e.*, when the tibia and metatarsus form their nearest approach to a straight line (Fig. 198); the movement is altogether too quick during the gallop. Its nearest representation is obtained when a horse 'stretches'; the limb is then thrust out behind, rigid and taut, and the hock fully extended. From the position of backward extension the limb is brought forward by flexion of the tibia on the femur, and the femur on the pelvis, by mechanisms already discussed, and flexion of the hock-joint follows (Fig. 197). The limb now comes forward under the body, and the foot, which was previously flexed, is extended, in order to come to the ground heel first or flat, depending on the pace. The leg is then in the position of forward extension (Fig. 199). While the extensor of the foot is producing this action with the assistance of the lateral extensor, the *flexor metatarsi* has to relax in order to unbend the hock. The flexor of the hock and the extensor of the foot have a common tendon of origin (Fig. 190), so that a remarkable physiological peculiarity now occurs, in that a pair of muscles having a common tendon of origin are enabled to function in a diametrically opposite manner, the extensor of the foot contracting, the flexor of the hock relaxing. The flexor of the metatarsus, apart from the common tendon at the femur, has a muscular addition from the tibia (Fig. 190), and it would be quite competent for this muscular portion to relax or contract independently of its neighbour. The difficulty lies in explaining the behaviour of the common tendon

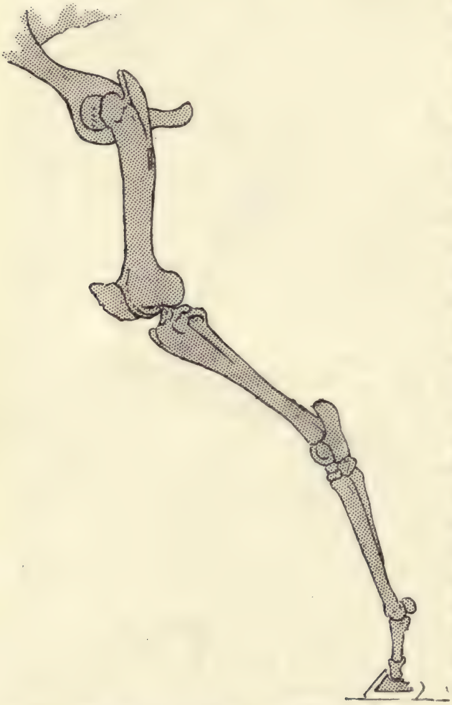

FIG. 198.—EXTENSION BACKWARDS OF THE HIND-LIMB.

to a pair of muscles running parallel to each other and functioning in an opposite sense.

Chauveau, many years ago, described the tendon of the flexor metatarsi as a conducting cord (Fig. 191, *3*), the function of which was to regulate the flexion of the hock by purely automatic action. He conceived that this automatic effect was brought about by stifle flexion. There can be no doubt that the position of the cord is greatly altered by flexion of this joint. The more the stifle is flexed, the higher the cord is drawn in the direction of the hip; and as it is fixed below to the metatarsus, the latter has to follow automatically (Fig. 197). But we cannot concur in thinking that the conducting cord can effect flexion without muscular aid, and believe that the *flexor metatarsi* must take an active share, in spite of the difficulty of explaining precisely how this is effected without inducing antagonistic action in its neighbour, with which, as we have seen, it possesses a tendon in common.

The next point to engage attention is the astragalus, the hinge-like ridges of which in the horse are arranged obliquely, like the threads of a screw. No other animal than the horse has oblique ridges to the astragalus. It might appear at first sight that their effect on flexion would be to turn the leg out below the hock. But the horse does not carry his legs in this way. When the hock is flexed, the parts below it are carried forward true to the front; if the ridges on the astragalus acted on the lower limb, the legs would be flung outwards. The screw of the astragalus affects the joint above and not the limb below it. It turns the stifle outwards, producing the stifle action so much admired in trotting horses. When the hock is flexed, the stifle

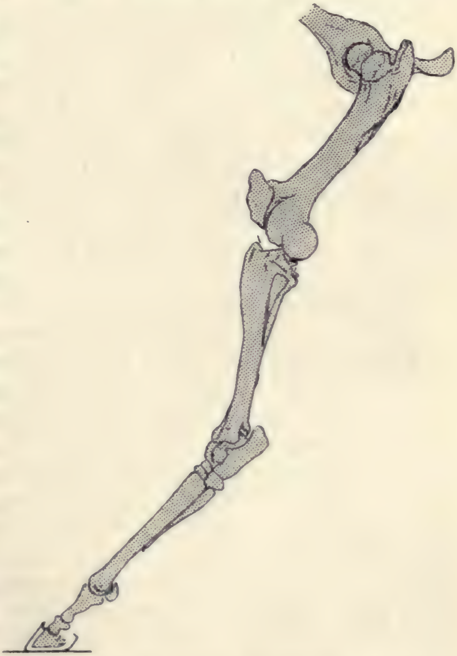

FIG. 199.—EXTENSION FORWARDS OF THE HIND-LIMB.

is turned outwards; when it is straightened, the stifle is turned inwards, and in some horses the effect of the screw-turning movement is to cause the foot, when it comes to the ground, to be twisted, and the point of the hock to be thrown outwards. This gives the appearance of a wrench, but is natural to some horses. Animals with a considerable space between the last rib and the stifle-joint do not need to have their stifles turned outwards. With the horse the last rib and stifle are so close together that the latter has to be directed away from the abdominal wall.

The movement between the small bones forming the hock-joint is very slight, and is not of a to-and-fro sliding motion, such as might be expected, but partakes of the nature of a rotation or twist on each other. This fact will be understood when it is remembered that the centres of the small bones of the hock are attached to each other, and to the astragalus and metatarsus, by interosseous ligaments centrally placed, which practically prohibit any movement but that of slight oblique twisting. The fact is also revealed by the friction marks in diseased joints.

The range of motion between the tibia and astragalus is considerable, yet it is not fully exercised in all paces. It is only in jumping and the gallop that the astragalus moves from end to end on the tibia. In order to prevent excessive flexion, two stops or buffers exist on the tibia, which come into contact with two rests on the astragalus. The outer stop is the larger of the two, but owing to the oblique face of the tibia, the inner one is the first to make contact. When the hock-joint is fully flexed, only the anterior part of the tibia is in contact with the astragalus; the posterior part is raised from the trochlea, and a space exists between them. The line of pressure through the hock falls mainly on its anterior part, and on the inner rather than the outer side. This is the region most frequently affected with disease. The tissues at the back of the hock suffer when the fore-hand is raised during jumping, and may also suffer strain when the hind-limbs receive the weight of the body in the gallop; but the chief trouble affecting the hock is that occurring to the bony structures.

The Functions of the Limbs in Relation to the Causes of Lameness.—The bones forming the flexible columns of the limbs, with their tendons, ligaments, and enveloping tissues, are exposed to strain. It is evident that the strain is greatest during movement, but it requires some little experience with horses to realise the stress the parts are exposed to even when the animal is doing no work. For instance, laminitis is common when horses are standing in a fixed position, as on board a ship, though nothing more than the weight of the body is being supported. A horse injured in one leg may frequently give way in its fellow through the latter supporting extra weight, so that, quite apart from work, the legs may suffer in their effort to support the weight of the body. During work the strain on the limbs is of two kinds—*i.e.*, that which arises when the body is propelled from the ground, and that which occurs when the body comes to the ground. One may be spoken of as the strain of propulsion, the other the strain of impact. Of the two, the strain of propulsion is the greater, and in consequence the limbs which propel the body during the fast paces suffer from injury to a far greater extent than those which receive it. Strain and concussion in the limbs are provided against in several ways. The bony columns of the legs, it will be observed, are broken up, the smallest segments being nearest the ground, the largest away from it. The bones forming the column are frequently arranged at an angle, by means of which direct jar is minimised. This is especially the case in the hind-limbs, which receive the weight of the body in all fast paces. Joints of a non-rigid kind are formed in three parts of the limb, all being close together and but a few inches from the ground. One exists within the foot, another at the fetlock, and an imperfect one at the pastern. These offer an elastic rather than a rigid resistance. The muscles, tendons, and ligaments also play their part. Muscles, we have seen, are perfectly elastic : it is a property which belongs to them ; neither tendons nor ligaments are regarded as elastic, though more than once attention has been drawn to the fact that there must be some give and take in these tissues, some stretching and recovery. That neither is capable of severe extension is undoubted, and normally, so long as the muscles maintain their complete command of the limb, both tendons and ligaments are subordinate to them in the matter of strain. When muscles tire and lose their elasticity, their tendinous attachments suffer, and it is practically only at this time that sprains of tendons occur. When a horse tires, it is the fore-leg flexors which sprain, for the reason that the burden of propelling the body falls on the flexor muscles of the fore-limbs ; the flexors of the hind-limbs only receive the weight when the body comes to the ground, and, relatively speaking, rarely suffer.

The extensor tendons of the limbs never suffer, for the work done by their muscles does not necessitate a powerful contraction such as occurs with the flexors when they propel in the gallop 9 hundredweight (460 kilogrammes) of material a distance of several feet through the air. This is why the flexor muscles tire in spite of their tendinous intersections, and the moment this occurs the tendons have to take the shock.* One can imagine that for some strides the check ligaments are useful accessories in helping the tendons to deal with fatigued elongated muscles, but the attempt to propel the body from the ground with tired muscles and a stretched tendon causes the latter to yield, and one or both partly or completely give way, either where the subcarpal check ligament joins, or between it and the fetlock. The muscles never rupture, and the tendons rarely yield at any other spot than between the fetlock and the middle of the shank. Both tendons in this region are practically at their smallest. Sprains of the flexor tendons do not occur at a walk, nor in the stable from slipping, nor on the road from trotting ; they occur during the canter and the gallop, for the reason that it is in these two paces only where one fore-leg is called upon to propel the entire body weight.* The suspensory ligament sprains when insufficient support is given by the tendons of tired flexor muscles to the fetlock and pastern. Other ligaments in the limbs may give way through an actual wrench—*i.e.*, the subcarpal ligament in draught-horses, caused by backing, or while endeavouring to prevent slipping on greasy roads ; but here the ligament is caused to act in an unnatural manner, both fore-legs being out in front of the body. Sprains of the connecting ligaments of the pastern-joint—viz., that formed between the pedis and corona—and some consider of the hock, may be due to wrenches during work, and form the origin of future disease in these regions. Lateral motion in either of these joints is normally very limited, and wrenches passing over broken ground must occasionally occur. Notwithstanding, the writer never remembers to have seen a case of non-traumatic lameness occurring to the pedal joint. The essential point, however, is that sprains of the flexor tendons or suspensory ligament, due to wrenches, are practically non-existent.

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* We have seen (p. 588) that there is a great difference between the post-mortem breaking-strain of the flexor as compared with the extensor muscles of the fore-limb.

The causes generally discussed above are mainly acting as the limb leaves the ground ; but there are others occurring during impact, producing what is conveniently termed ' concussion.' These jar the foot and the bones at the lower end of the column. Of this the clearest evidence is furnished by fractures of the pastern, which always occur as the foot comes to the ground. When the suffraginis, and rarely the corona, break, the line of fracture is in nearly every case very similar, showing either that a common cause is at work, or that these bones possess inherent lines of weakness.

We have glanced at two periods during locomotion when injury may occur ; there is one other, and that is the time during which the body is rotating over the foot. It has been shown that the fore-leg below the elbow is only intended to open and close in one direction ; for instance, the foot may be made to touch the back of the elbow, but it cannot be made to touch the front of the knee. When the body is rotating over the foot, a point is reached where the bones between the elbow and the foot are locked together and rotate as one piece (see p. 609). At this time there is a great strain on the locking arrangement, and considerable compression of the small bones which form the end of the limb. Between the suffraginis and corona the strain would appear to be the greatest, on account of the small size and slender nature of the joint, and for the reason that it is placed next to the centre of rotation. Clinically it is recognised that this region is the seat of often incurable lameness.

There are some seats of lameness where apparently specific causes are at work which should not baffle discovery. It is the upper and *never* the lower articulatory surface of the corona which is involved in ringbone, though the ends are only an inch or two apart ; it is the under and *never* the upper surface of the navicular which is affected with caries, though these surfaces are not ½ inch away from each other. It is the inside and *not* the outside of the hock-joint which is affected in spavin. The seats of these affections are not matters of accident, but due to definite causes which the writer considers are intimately concerned with the physiology of the parts.

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* The flexor tendons of the American trotting horse give way, though not so frequently as in race-horses in this country. It occurs when the animal tires. It has been said above that horses do not sprain their tendons while trotting, but obviously this does not refer to racing. Further, the animal, when match-trotting, does not use his limbs in the same way as in the common trot. On this important point, see p. 624. The writer is indebted to Professor Pierre Fish, New York State Veterinary College, Cornell University, and to Drs. W. Sheppard, M.R.C.V.S., and Grenside, U.S.A., for information regarding lameness affecting the American trotter.

In concluding this brief outline of the physiological aspect of lameness, attention must be drawn to the fact that it is the small and not the large joints which usually suffer ; it is not those at some distance above, but those nearest to the ground. It is not the fibrous tissues so frequently as the denser structures. Speaking generally, three-fourths of the cases of lameness occur in the fore-limb, and three-fourths of the lameness in the fore-limb occur within a few inches of the ground. The detection of the seat of lameness will ever be one of the most difficult duties of the veterinary surgeon, and a thorough knowledge of the anatomy and physiology of the limbs is the first step towards forming a sound judgment.

SECTION 2.

Locomotion.*

The movement of the limbs during locomotion is a question both of theoretical interest and practical importance. This is especially so in the case of the horse, owing to the fact that he is one of the few domesticated animals which has to work, and the frequency with which this results in lameness. There are features connected with lameness which can only be explained when the method by which the limbs are employed during progression is understood. Limb movements in the biped are relatively very simple ; in the quadruped there is both simplicity and complexity, the latter owing to the rapidity of movement and the inability to watch four legs at one and the same time. All paces but the simple trot defy accurate visual analysis. It was not until instantaneous photography came to the aid of physiology that the question of the sequence and method of limb combinations during locomotion was finally settled. The name of Muybridge and his co-workers will for ever remain identified with this inquiry. Without instantaneous photography it would have been impossible to analyse fast paces like the gallop, though it is distinctly remarkable how very close some of the older observers got to the truth. Exactitude, however, was not obtained, nor criticism silenced, until 1878, when the camera, under the direction of Muybridge, set the question of animal locomotion for ever at rest.

Step and Stride.—When a man walks, the *step* is the distance between the two feet measured from toe to toe or other convenient but identical point ; two such steps constitute *a stride*, which is the distance covered by a foot from the time it leaves the ground until it again reaches it. With quadrupedal locomotion the same definition holds good, but the introduction of another pair of legs renders it rather more complex. With the quadruped the **step** is the distance between any two hind-limbs or any two fore-limbs, or any fore and hind limbs employed in moving together. The **stride** is the distance covered by a fore or hind limb from the time it leaves the ground until it again reaches it. The step and stride can be measured by the impressions left on the ground, though they require great care in order to discriminate carefully between the various feet. In the same horse a step from one hind-foot to its fellow is not always the same length as a step from one fore-foot to its fellow. In the faster paces like the gallop the step taken by the fore-legs is longer than that taken by the hind-legs. In the horse one stride at a walk contains two steps ; in any faster pace than the walk the stride embraces a period in the air, during which there are no feet on the ground. In the trot, the legs being used in diagonal pairs, there are two steps and two springs to the stride ; in the canter and gallop there are two steps and one spring.

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* I have to thank Majors F. W. Hunt and Edwards and Captain Wadley, A.V.C., for many observations they have made for me on this subject.

Limb Velocities.—It must not be forgotten that in the slowest paces the legs in motion are moving faster than the horse. Take the case of the walk at five miles an hour : the moving legs have to overtake the body, and in order to do that within the brief period allowed they must move at least double as fast as the horse. In the gallop Muybridge showed that a horse covering nineteen yards in a second (thirty-nine miles an hour nearly) the advancing limb was brought forward with an occasional velocity of forty yards a second, or nearly eighty-two miles an hour. It is not a matter for surprise that so much doubt and difficulty existed before the introduction of instantaneous photography.

The ordinary exposures given by Muybridge were the one-thousandth part of a second, though much shorter exposures than these were also employed. During the one-thousandth part of a second a horse galloping as above may move forward $\frac{7}{10}$ inch, and the moving foot $1\frac{1}{2}$ inches, so that shorter exposures had to be employed for high velocities.

Even when the order and method of moving the limb is known, it is very difficult, excepting in the slowest paces, to catch a glimpse of the real movement in any other pace than the trot. The limbs are as confusing as the spokes of a rotating wheel, while the body of the horse itself helps in no slight way to divert attention. To obviate this the writer finds that the best method of seeing the limbs working is by looking at them through a narrow slit in a card, so held that only the legs are seen through the slit and the body cut off.

The paces commonly employed by the horse are the walk, trot, canter, and gallop. There are others, such as the amble and the rack, neither of which are popular in this country, nor, indeed, is the latter employed for any other purpose than in one form of American racing. In all these paces the limbs are employed in different combinations. In the walk, for instance, a broad base of support is required, so that during a stride for half the time there are two legs and half the time three on the ground at one and the same moment. In the trot for half the time there are two legs on the ground and half the time the body is in the air. The arrangement is different in the canter, and again different in the gallop. Each pace has its own system of combinations, and when all the possible combinations are classified they amount to fourteen for the four legs. For intance, the number of different ways in which a single limb may be employed is obviously four, the possible combination with two legs is six, and the various combinations with four legs employed in progression is fourteen.

The Walk.

This pace is relatively slow; an ordinary horse walks about four miles an hour, and it would seem that, considering each limb can be distinctly observed, its movements would be easy to follow. As a matter of fact, to watch them is bewildering. The walk begins from a fore-leg. If a horse from rest begins to walk, one or the other fore-legs will be found the first to advance; there is no special choice shown as to whether it will be a near or an off leg, though an animal may time after time start with the same limb. This is not the generally accepted opinion outside the veterinary world. Muybridge himself says:

> 'When a horse is standing with the weight of the body equitably distributed over his fore-legs, and under these conditions commences to walk, the initiatory movement will invariably be made with a hind-foot.'

Borelli, who wrote on animal mechanism towards the end of the seventeenth century, described the walk as beginning with a hind-foot, but this has never been accepted by any veterinary writer. Percivall and Gamgee especially attacked it. Hayes says: 'As a rule a horse begins the walk with a fore-leg.' This suggests he has seen a hind-leg initiate the movement—in fact, he describes the sequence of limb movements which occur when a hind-leg is the first to start. It seems a remarkable fact, when all the most difficult questions connected with locomotion are settled, that the simple one discussed above is not satisfactorily determined. In consequence of the opinion of Muybridge we are unwilling to deny that the movement, though commonly beginning with a fore-limb, may be started by a hind-leg, though in the experience of the writer and those who have observed for him the movement invariably begins in front, and never behind, unless the horse is 'reining back.' The first step taken in walking backwards is always taken with a hind-limb, which appears to support the view that the first step forwards is always made with a fore-limb. On the other hand, the first step in draught may be taken with either a fore or a hind leg; the former if the draught is easy, the latter when it is heavy. In 'backing' in draught a hind-foot is first moved if the load be light; if heavy, the animal leans well back and moves a fore-foot first. If the horse's head be placed uphill he starts with a fore-leg, provided the hill is not steep; if steep, he starts with a hind-limb. When the head is downhill the first step is taken with a fore-leg.

A fore-limb having initiated the movement, the next leg to take part is the diagonal hind; for instance, if the step begins with the off fore, as in Fig. 200, (1), the next leg to move is the near hind (2). This is followed by the near fore, and lastly by the off hind. There are four distinct movements in each stride of the walk, and as there are two strides to a complete advance of the body—viz., one on the near and one on the off side—there are altogether eight movements. The best method of conveying the eight movements of the walk is by means of a system of notation,* as in Fig. 201. This shows that in the walk the limbs on the ground at any one time are three, followed by two, followed by three, and so on. In Fig. 200, (1) shows that the support may be by means of one fore and both hind legs, or one fore and one hind diagonal, as in (2), or both fore and one hind, as in (3), or one fore and one hind lateral, as in (4).

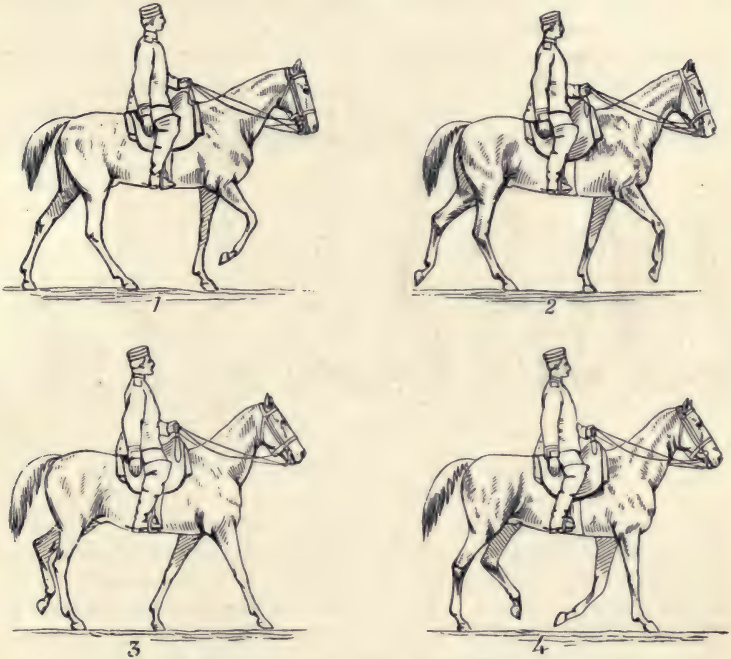

FIG. 200.—THE WALK (ELLENBERGER).

There may be slight variations in the walk, such, for instance, as in the case of a draught-horse loaded or a horse out grazing; but in the true walk the broad principles above described are never departed from. In Fig. 201 may be seen some of the features of the horse's walk. It will be observed that the three limbs followed by two is the characteristic, the three limbs being any three, the two being any two, provided one is a fore and one a hind. The track left by a horse at the walk is shown in Fig. 212. If a track be studied, it will be observed that the impression of the hind-foot is generally in advance of that of its fore-foot, the limbs being in the position of the near legs in Fig. 200, (4). But there is considerable variation; the hind-foot in a good walker will always be placed down in advance of the impression left by the fore-foot. In an average walker the hind-foot impression covers the fore more or less; in a horse that is a bad walker, or is tired, or taking short steps for any reason, as in heavy draught, the hind-foot impression is behind the fore. In draught it comes behind the fore if the traction be heavy; in descending a hill, it comes behind the fore if the load is under control, but it falls in front of it if the weight cannot be properly held back. The fore-leg remains on the ground for a longer time than it takes in passing through the air, and comprises the period during which the body is passing over the limbs. The movement in the air of both fore and hind legs is so extremely rapid as almost to defy detection. The snatching up of the foot from the ground is the quickest movement.* Muybridge, following Gamgee (senior), refers it to the spring or rebound of the suspensory ligament, but it would seem to be due entirely to the flexor muscles. In walking on level ground the majority of horses rarely extend the knee any great distance beyond a vertical line dropped from the point of the shoulder.

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* In the diagrams of notation the narrow end of the figure represents the head; the spots represent the legs on the ground at any one moment; they do not, of course, represent the relative position of these limbs to each other.

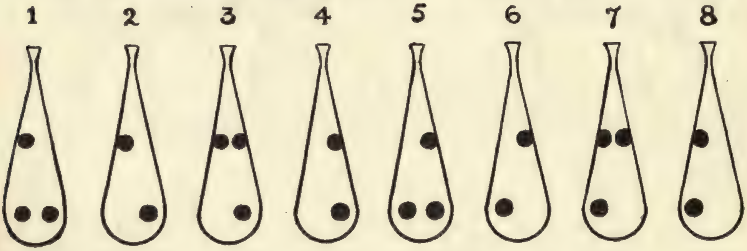

FIG. 201.—NOTATION OF THE WALK.

1, 2, 3, and 4 correspond to similar numbers in Fig. 200.

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* The writer caused horses to trace this movement by fixing a pencil to the foot and walking them past a piece of prepared canvas arranged vertically so as to act as a recording surface. There was a good deal of variation in the character of the curves, depending upon the part of the foot to which the pencil was attached, a toe curve being different from one taken at the quarter.

A sudden movement of the extensors now straightens the limb, and the foot is placed down flat or heel first. If the leg is not fully straightened by the extensor muscles, the foot comes to the ground toe first, with the knee slightly bent, and a stumble follows. In heavy draught-work it is no uncommon thing to see the toe put down first, but here the conditions are very different. Some horses walk with a pair of lateral legs, both off and both near alternately. The camel employs lateral legs as a natural means of walking.

The walk is a most important pace; few horses are capable of walking well, but it can be greatly improved by education. The ordinary saddle-horse has a *stride* of from 5½ to 6 feet (1·67 to 1·83 metres) at a walk. A *step* made either by a pair of fore or a pair of hind legs varies from 33 inches to 39 inches in length (·84 to 1 metre).

The Trot.

A trot may be described as slow, ordinary, and flying. In the latter there is a slight difference in the support given the body, but in the other two the movements of the limbs are identical. The trot is a very simple pace to observe, inasmuch as the legs are worked in pairs, so that instead of four moving in different times, there are two moving together. The two are *diagonal* legs, one fore and the opposite hind. These thrust the body forwards off the ground, and it is received on their fellows, which repeat the movement. During each thrust there is a period during which the body is in the air and no legs on the ground. In the trot there are two steps to the stride, and two periods in each stride that the horse is in the air; the steps are always with diagonals, as shown in the notation in Fig. 202. In Fig. 203 some of the characteristic phases of the trot may be seen. In (1) the horse is on diagonals; in (2) he has propelled the body forward and off the ground; in (3) the animal has alighted on the opposite pair of diagonals; and the process is then repeated. In America the flying trot has long been cultivated, with the result that some remarkable velocities have been

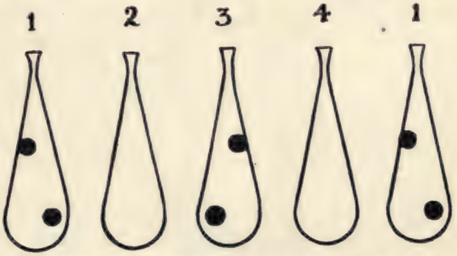

FIG. 202.—NOTATION OF THE TROT.

In (1) the body is being propelled by diagonal legs; (2) the body in transit and off the ground; (3) it is received by opposite diagonals, and again propelled.

obtained. The limb movements are not quite the same in the match-trotter as in the ordinary trotter. Muybridge shows it as follows (Fig. 204). The difference between match and ordinary trotting is that the match-trotter does not leave the ground simultaneously with a pair of diagonals, but with one at a time, nor does he arrive on the ground with a pair, but with one at a time. The interval in time between the arrivals is extremely small, but it distinguishes the flying from the ordinary trot. In the ordinary trot, it will be observed, the body is propelled by a diagonal fore and a hind leg simultaneously, but in the match-trotter the propelling is done first by a fore and then by a hind. This action of the hind-legs as propellers is important to notice ; it does not occur in either the canter or the gallop, but appears again in the jump. It will also be noticed that the body, on coming to the ground, is received first by a fore and then by a hind limb. In the ordinary trot it is received by fore and hind limbs simultaneously.

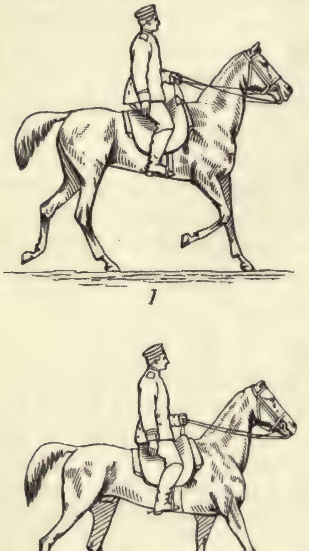

Fig. 203.—The Trot.

From instantaneous photographs by O. Anschütz. (Ellenberger.)

The velocity trotting horses attain is quite remarkable. The historic horse Edgington, the first to be photographed while moving, and whose stride when exhibited on paper revolutionised the public conception of animal locomotion, was taken while trotting the mile in two minutes sixteen and one-fifth seconds.* The length of the stride was 17 feet (5·15 metres), and the space traversed during the time the body was travelling through the air with no feet on the ground—viz., the period of suspension—was 5½ feet (1·65 metres) at each step. This may be compared

* Higher velocities than the above are common in American racing. The mile has been done in less than two minutes.

with the ordinary saddle-horse, which has a *stride* at the trot of 9 feet more or less. The length of a step taken either by a pair of fore or hind legs rarely reaches 5 feet, and is generally about 4½ feet in length. The foot-tracks made on the ground by a horse trotting are shown in Fig. 212. In the trot the impressions of the hind-feet are generally made over those of the fore, but not always, as may be seen in the case of the off fore in the figure. The only real difference between the tracks of the horse trotting and the one walking lies in the interval between the feet—*e.g.*, in the length of the step and stride. The height of suspension in the air is greatly exaggerated in the trotting horse. In the ordinary horse it may scarcely be noticed, the feet only being lifted sufficiently high to prevent them being dragged over the surface of the ground. The distance covered during suspension is that which separates the fore from the hind legs; if these are between 3 and 4 feet apart, that is the distance covered while the animal is in the air. This will be realised from an inspection of Fig. 203 (2), in which the body is shown suspended, having just been propelled by the united action of the near fore and off hind. The off fore and near hind are coming to the ground, and we know from our study of the foot-tracks that the latter will be placed over the spot just occupied by the near fore foot.

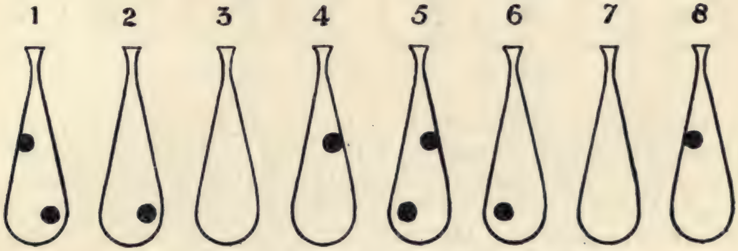

FIG. 204.—NOTATION OF AMERICAN TROTTING HORSE.

(1) The diagonals are preparing to propel; this is effected first by a fore-leg, one hind being left on the ground (2); the thrust from this lifts the body off the ground (3); it is then received on one fore-leg (4), and then by the diagonal hind (5). From this point the movement is a repetition of (1).

When a horse falls at the trot, he does so either through not flexing his knee sufficiently before bringing the leg forward, or the extension of the knee is not perfect, and in consequence the limb is unfit to stand weight. The knee should be sufficiently but not unduly bent and the leg brought rapidly forward; the limb is then sharply extended, well braced, and the foot placed firmly on the ground heels first. Regarding the latter point, the question of pace settles whether the heel is distinctly the first to make contact. In photographs of the match-trotter the inclination of the toe upwards as the foot comes to the ground is very marked. In slower trotting the foot comes down flat, but with always an inclination for the heel to make the first contact. When a horse is inclined to come on to the toe instead of the heel, he at once stumbles, and this occurs when the muscles tire, when the feet are too long, or the mobility of the joints impaired.

The **Amble** is the nearest approach to a run ; it consists of a short, quick series of steps, in which lateral and diagonal legs are alternately employed, with no period of suspension—*e.g.*, there is no period during which the body is left without a leg on the ground. It is best studied from the notation in Fig. 205, which shows that it is executed by a pair of laterals, followed by a single fore lateral, succeeded by a pair of diagonals, followed by a single hind-leg and then a pair of laterals. From the fact that there is never a period during which the body is without support, the pace is an easy one for the horse ; and as there is no thrust upwards into the air, it is an especially easy pace for the rider, who barely moves in his seat.

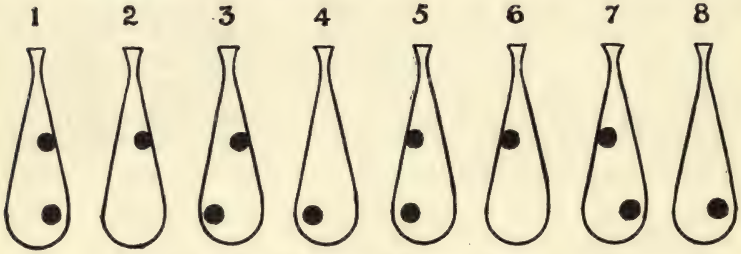

Fig. 205.—Notation of the Amble.

In **Pacing** or **Racking** the horse, instead of using diagonal legs, uses the lateral limbs, so that off fore and off hind are on the ground instead of off fore and near hind (see Fig. 206). An animal may 'pace' both at the walk and trot, in this respect resembling a camel. There is no doubt that it is a perfectly natural movement for some horses ; others are taught it. Some extraordinary velocities are recorded in America with this gait. In fast paces the horse oscillates from side to side ; the appearance is very unsightly, and racking is not encouraged in preference to trotting. A defective leg which will not stand trotting may stand 'racking.'

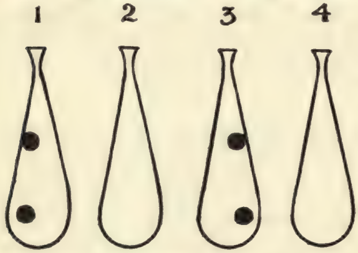

Fig. 206.—Notation of the 'Pace' or Rack.'

The Canter.

This is a pace entirely different from any previously considered. To make the canter clear, it must be remembered that the body is propelled forward by one fore-leg, and no matter which of the two it may be, it is received on coming to the ground by the opposite or diagonal hind-leg. There is no exception to this rule, which will be found equally true for the gallop. It is well to get this fact clearly established (see Fig. 208). In (1) the animal is propelling the body off the ground with the off fore-limb, and in (3) alights on the near or diagonal hind-leg. The importance of the principle of the employment of diagonal legs will be observed; we have seen it in the walk, it is the essential feature of the whole movement in the trot, and we now meet with it in the canter. The notation of the canter is shown in Fig. 207.

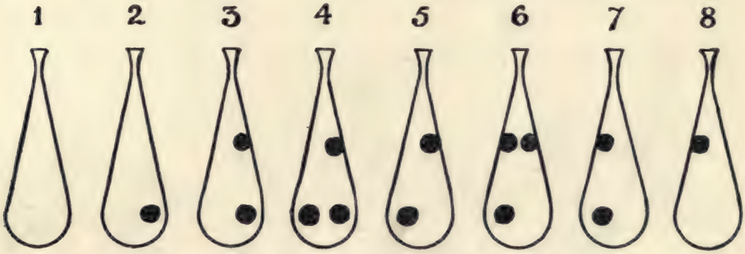

Fig. 207.—Notation of the Canter.

It starts from the moment the body is in the air (1), where it has been propelled by the leading fore-leg*—in this case the near. The animal alights on one hind-leg, the off (2), the diagonal to the leading fore-leg; this is followed by the fore-leg on the same side—viz., the off—coming to the ground (3), so that for a very brief period the body in the canter is supported by lateral legs. The next change is that the fellow hind-leg comes to the ground (4), the body now being supported on one fore and both hind limbs; the hind-limb which first received the weight is then withdrawn (5), and the animal is left on diagonals. This is followed by the leading fore-leg coming to the ground (6), so that the body is now supported on both fore-limbs and one hind-limb. The off fore-limb is next withdrawn, and the animal is left on lateral legs (7); the near hind is withdrawn, and the horse left on one fore-leg (8), which, as we have seen, is the leading or propelling limb. This sounds very complex, and there is no doubt that the canter is difficult both to analyse and describe. It will be observed

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* The leading fore-leg in the canter and gallop is the one which gives the final propulsion; it is the leg which does all the work. When going straight, either fore-leg may lead, and a well-trained horse should be taught to save leg weariness by changing the leading leg. In turning or moving on a circle to the left, the leading leg must always be the left; similarly, in circling to the right, the leading leg must be the right.

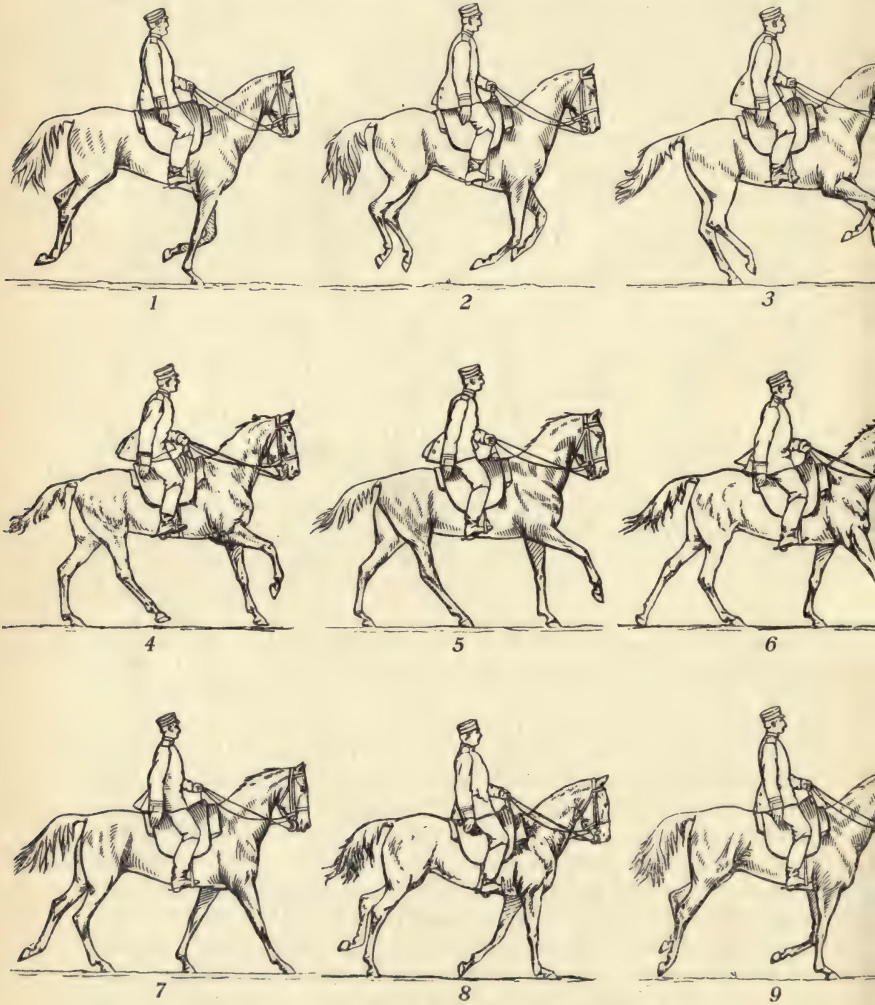

Fig. 208.—The Phases of the Canter (Anschütz).

that in the seven sequential movements connected with the canter the body is twice—viz., at the beginning and end of the movement—on one leg; at two periods it is on two lateral legs ; at two periods it is on three legs ; and at one period on diagonal legs.

Turning now to actual photographs of these movements, Fig. 208 (1) shows the propulsion from the ground by means of the off fore-leg ; (2) represents the animal in the air ; (3) shows the horse alighting on the near or diagonal hind-leg ; (4) exhibits the animal standing on two lateral legs, the off hind, it will be observed, not yet having reached the ground. In (5) the body is on three legs, both hind and near fore ; in (6) the animal is on diagonal legs, near fore and off hind only : the toe of the near hind is just leaving the ground. Had the picture been taken the minute fraction of a second later, this foot would have been seen off the ground. The animal, however, is clearly on diagonal legs, for a hind-leg thrust as far back as that shown in (6) is of little support. In the next figure (7) the off fore-leg has come to the ground, and the horse is standing on three legs. Of these, first the near fore (8) is snatched up, leaving the body balanced on both lateral legs, followed by the off hind (9), which leaves the animal on one fore-leg, the off, preparatory to the final spring, which is farther advanced in (1), and actually occurring in (2).

The canter is an easy pace for the rider, owing to the number of limbs supporting the body in turn, as many, in fact, as in the walk ; it is this which gives smoothness to the working. To obtain smoothness the limbs must follow in definite order. A horse that can only canter with the off fore leading is anything but comfortable when he tries to lead with the near fore ; it is impossible for him to group his legs in the correct order —everything is disjointed owing to want of proper co-ordination. It should form an essential part of the training of every saddle-horse to teach him to lead freely with either fore-leg. In this way he will change as one leg tires, and so save himself from a sprained limb.

The essential features of the canter being a hind-step, a fore-step, and a spring, it is desirable to glance at the value of these in an ordinary horse. The step with either a pair of fore or hind legs varies from 37 to 43 inches in length. The stride varies from 9 feet 8 inches to 11 feet 8 inches. The difference in the length of the stride does not depend so much on variations in the length of the step as in marked variations in the distance of the spring. In a slow canter the spring may be ½ foot or even less, whereas in a fast canter it may be 2 feet or more. The tracks left by a horse cantering are shown in Fig. 212. The length of this horse's stride was 10 feet 8 inches, and the spring forward was 6 inches.

The Gallop.

Muybridge points out that all animals do not gallop alike—that is to say, by means of identical leg movements—nor, in the case of the dog, does the same animal always gallop in the same way. There are two distinct gallops described by Muybridge: one he calls the *transverse*, the other the *rotatory* gallop. In Fig. 209, A, the scheme of a transverse gallop is shown; in B that of a rotatory gallop. The horse always employs the transverse, while the dog and many other animals use the rotatory gallop.

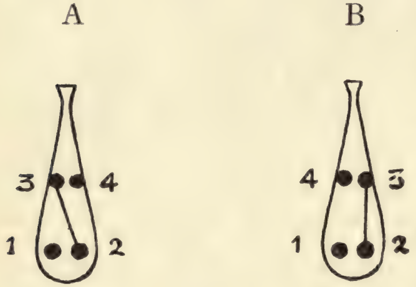

FIG. 209.—SCHEME OF THE GALLOP.

A, Transverse gallop; the legs move in the order of the numbers. B, Rotatory gallop.

To understand the gallop it is essential to remember that the propulsion or spring is done by one fore-leg, and, as in the canter, the body alights on one hind-leg, which is always the diagonal one to the propeller. The body, having alighted, a step is made with its hind-legs, then a step with the fore-legs, from which it is again propelled. As in the case of the canter, there are two steps and a spring in the stride. There are seven different positions assumed by the legs during the gallop, which may be seen in Fig. 210. Beginning with the body in the air, as in (1) the animal alights on one hind-leg (2), in this case the near, as the leading leg was the off. This receiving leg is thrust well forward under the body, in great contrast to the canter, and for a minute period the animal is standing on one leg; the opposite hind-leg then makes a step and comes to the ground (3): the body is now momentarily on two hind-legs. The fore-legs have

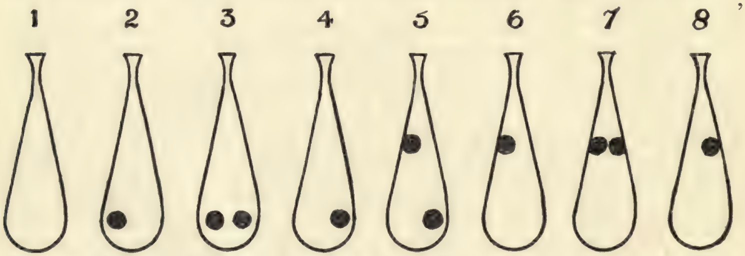

FIG. 210.—NOTATION OF THE GALLOP.

not yet reached the ground; they are being advanced as far as possible to the front, and to enable them to reach forward the first hind-leg is snatched off the ground, and the animal is again left standing on one hind-limb (4). The fore-legs now begin their descent, and the one diagonal to the hind-limb on the ground now makes contact (5). The horse's body is then supported on one fore and one hind diagonal legs. It is now the turn of the fore-legs to make their stride, and to effect this the body rotates over the fore-leg, and in doing so the hind-leg leaves the ground. The animal is once more left on one leg (6). The step is now made, both fore-legs being on the ground (7); the first fore to reach the ground is now snatched up, and the horse is left standing on one leg (8), which is the leading one, and within the next fraction of a second the body is in the air. In Fig. 211 each of the important movements is shown in the horse. (1) is the body in the air; the manner in which the legs are collected under it should be particularly noted; the hind-limb which is about to make contact is thrust as far forward as possible. In (2) this limb has reached the ground; in (3) its fellow has arrived, and the step with the hind-legs taken; in (4) the big reach forward has occurred, to effect which one hind-leg has been withdrawn; in (5) the body is rotating over one fore-leg in order to make its step; at (6) this step has nearly been effected; at (7) the step has been taken, and the fellow fore-leg withdrawn; the body has now rotated over the leading leg at (8), and when this has been completed the spring into the air is made. The gallop is an easier pace to follow than the canter; there are never more than two legs on the ground at any time, and the greater part of the work is done with one leg. Briefly, a hind-step with no support in front, a fore-step with no support from behind, and a spring, constitute the essential features of the movement. The only time when the hind-leg gives any assistance to the fore-limbs is when one of the latter makes the forward reach preparatory to taking its step. When a horse gallops, no matter how fast, the fore-feet never extend in front of a vertical dropped from the muzzle. In Fig. 212 is shown the track left on the ground by a galloping horse. Muybridge, working with an average thoroughbred in racing condition, galloping at the rate of thirty-five miles an hour, obtained the following results: Length of stride, 22 feet 10 inches, made up as follows:

Fore-step	5 feet	0 inches.
Hind-step	3 ,,	10 ,,
Interval between hind and fore legs	7 ,,	6 ,,
Spring	6 ,,	6 ,,

With the ordinary horse, the strides of which vary from 15 feet to 19 feet, the following results were obtained:

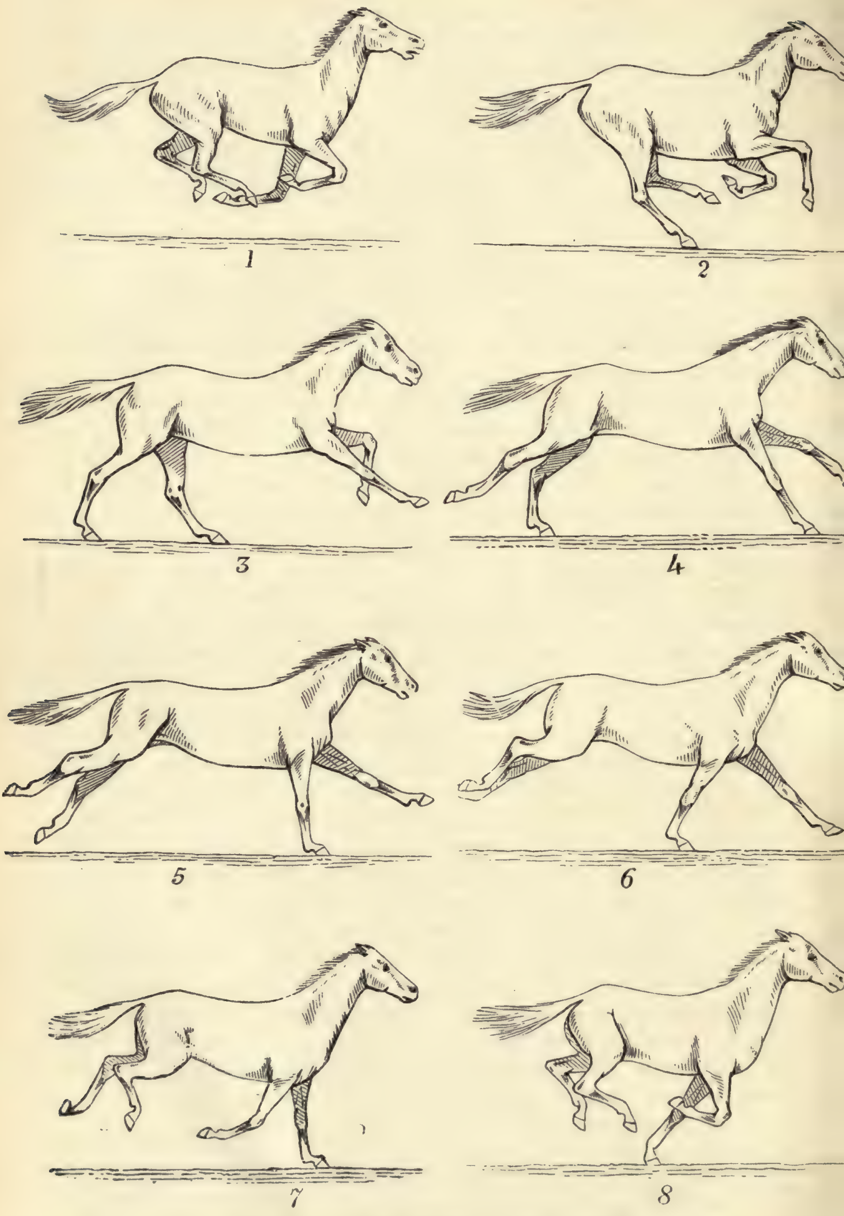

Fig. 211.—The Phases of the Gallop.

After Stanford, Muybridge, and Stillman ('The Horse in Motion').

Fore-step	3 feet 5 inches	to 4 feet 3 inches.
Hind-step	2 ,, 11 ,,	to 3 ,, 11 ,,
Spring	2 ,, 11 ,,	to 6 ,, 2 ,,

Here, again, it was shown that the difference in the length of the stride is not so much the difference in the length of the step as in the distance of the spring. The forward reach, such as the horse is making with the off fore in Fig. 211 (3) is of much the same length in ordinary animals—*e.g.*, 5 feet 5 inches to 6 feet—though occasionally as much as 6 feet 6 inches. In the race-horse above referred to it is 7 feet 6 inches. It will be observed that both with the race-horse and the ordinary horse the step taken by the fore-legs in the gallop is longer than that taken with the hind-legs.

Differences between the Canter and Gallop. — In the canter it can be seen thatthe horse makes a big step first with his hind-legs, then with the fore, followed by a spring ; he is only once in the air in each stride. In the gallop the same essential features occur ; but the canter differs from the gallop in being a slower pace : the hind-leg, in order to receive the weight, is *not* brought well under the body (see Fig. 208, 3), and in consequence the lateral fore-leg has to come to its assistance, to enable the hind to complete its step. There is no such support given with a fore-leg in the gallop. In consequence of the slowness of the canter, one hind-leg has now in turn to help support the body while the fore-legs make their step, and this support is not withdrawn until the one fore-leg is ready to make its spring. No such hind support exists in the gallop during the period the fore-legs are making their step. In the gallop there are never three legs on the ground at one and the same time ; in the canter this occurs twice in a single revolution.

The conventional gallop shown in pictures is much more pleasant to look at, but wholly incorrect. F. Galton* observed that the two fore-legs in the photographs of the gallop were extended during one quarter of a complete motion, and during another quarter the two hind-legs were similarly extended ; cutting them in halves, and uniting the front half of the former to the hind half of the latter, a fair equivalent of the conventional attitude was obtained. He considered that, owing to the confusion created by the limb movements, the brain ignores one half of all it sees, and divides the other half into two parts, each alike in one particular, and then combines the two halves.

The **Gallop of the Dog** is rotatory, as Muybridge terms it (Fig. 209, B), and the grey hound gallops differently to a heavy dog. The latter employs the gallop of the horse, excepting that the animal alights on the lateral and not on the diagonal hind-leg ; the opposite hind-leg then comes to the ground, next the fore-leg of that side, then the opposite fore-limb, followed by the spring. The order is, therefore, as follows, assuming the thrust is given with the left fore-leg : left fore, left hind, right hind, right fore. As in the horse, there is a step with the hind followed by a step with the fore legs, then a spring. The movement of the limbs of the grey hound also follows in the order left fore, left hind, right hind, right fore ; but there are two periods of propulsion : first with a fore-leg, which sends the body into the air with the fore and hind legs crossed like a pair of scissors; next a thrust with a diagonal hind-leg, which shoots it once more into the air, alighting on a lateral fore-leg. Consequently, in a single stride of the greyhound there are two springs, once from a fore-leg and once from a diagonal hind-leg.

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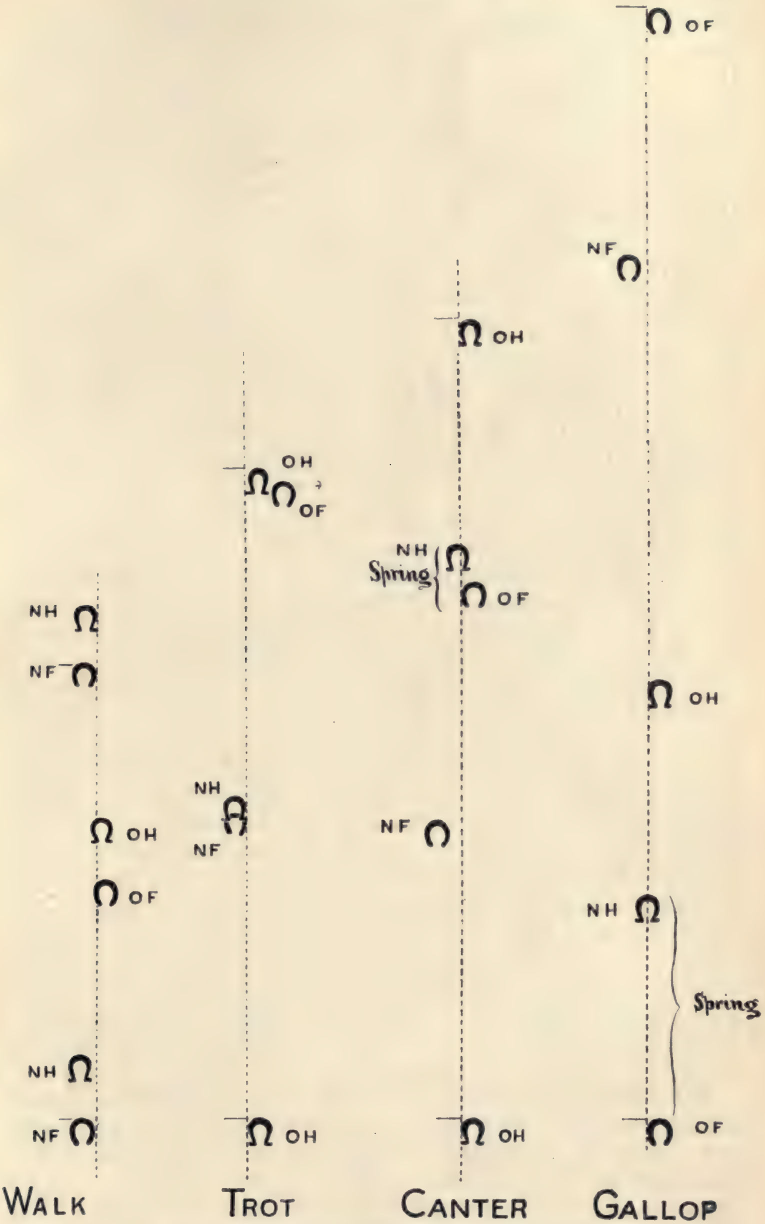
* "Memories of My Life," 1908.

The **Footprints** occurring during the various paces of the horse have been previously referred to; they are illustrated in Fig. 212. Before the days of instantaneous photography a great deal of attention was paid to them as a graphic record of locomotion, and nothing, perhaps, better illustrates how differently horses move while performing the same pace, or even the same horse at different times. The differences do not, of course, lie in the modes by which the limbs are moved, but the length of the steps taken and the position of the feet relative to the central line of the body. In the walk, for example, the hind-feet may be placed down immediately on top of the impressions of the fore, or they may be placed in front of or half covering the fore-prints. The only real interest now attached to a study of footprints lies in the information they furnish of the extent to which the feet are brought under the middle line of the body as a means of support. This is ascertained by the use of a line so adjusted as to lie midway between the tracks made by the near and off feet. Such a line represents the middle line of the body. It might at first sight be reasonable to suppose that the off feet would fall to the right and the near feet to the left of such a line, and that the distance the impressions were made from the central line, would be represented by a line passing midway between the feet during repose. But this is not so; a pair of fore-feet 5 inches apart during repose, may be shown during locomotion to be brought completely under the middle line of the body, or even to cross it. During the slowest paces the feet are planted very nearly or quite in a line with the centre of the body; during the faster paces they may be brought so far under from each side as to cross the central line. In the gallop the feet are brought well under the central line of the body, forming a very straight track, occasionally broken by being planted away from the centre, or sometimes completely crossing the centre to the opposite side of the body. All the features discussed may be seen on inspection of the various foot-tracks shown in Fig. 212. The dotted line represents the middle line of the body.

Summarising these results, we see that, though in repose the feet may be 4 or 5 inches apart measured from their inside edge, the tracks these feet leave on the ground do not show this interval; on the other hand, they are brought well under the centre of the body, sometimes even crossing it, and the faster the pace, the nearer the footprints approach a straight line. It is obvious that the more the feet are brought under the middle line of the body, the more stable the support afforded, but it is not clear how they are able to avoid striking their fellows.

The Jump.—It is said that no two horses jump alike, and even that the same horse under identical conditions will jump differently. The differences alluded to originate in the manner in which the hind-legs are handled preparatory to collecting the body for the spring upwards. Under ordinary circumstances, as the jump is approached, the animal is steadied in his stride, in order to afford him the needful opportunity of 'collecting'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OH
OF
WALK
TROT
CANTER
GALLOP

FIG. 212.—FOOT-TRACKS AT VARIOUS PACES.

A stride is indicated by the line at the toe of identical feet. These tracks were furnished by the same animal.

himself and forming his judgment of the obstacle. During the steadying period he is getting ready to raise the fore-hand: this he could not properly effect without a modification of the pace; he is also estimating at what point he should take off. In Fig. 213, (1) and (2), the horse is seen steadying himself, bringing the hind-legs well under the body, and raising the fore-hand. In (3) the final upward push has been given by a fore-leg, and in this process not only the fore-legs but the muscles of the back and loins are playing a most important part. It is impossible for a horse to rear even to the partial extent required for an ordinary jump if the back is weak. In (3) the obstacle is being faced, the animal is lifting the fore-hand and bending the knees, the hind-legs being well under the body, in order to support the weight. The next important point is the continued bending of the knees in (4) and the straightening or extension of the hind-legs. The moment the fore-feet are above the level of the obstacle, propulsion forward with the hind-legs begins; first both hind-legs straighten themselves, extending to the utmost, while the limb nearest the jump is left to give the final push off (5) and (6). It is now the turn of the hind-legs to become flexed, the hocks bending as much as the knees had previously done, while at the same time the fore-legs now extend, with the object of making contact with the ground. This contact must be made with a firm, straight leg, one (6) followed by its fellow (7), which in (6) is seen placed out in advance. It is advanced in order that the first fore-leg to make contact (6) may be carried forward out of the way (7), for it is occupying the place where the hind-feet will alight. These now come down, first one, then its fellow, but before the second hind-leg reaches the ground the fore-leg has already pushed off (8). It will be observed that the jump resolves itself into a partial rear, a doubling up of the fore-limbs and powerful extension of the hind, followed by the upward push, the extreme flexion of the hocks, the marked extension of the fore-legs, and the reception of the weight of the body on first one and then the other fore-leg. The jump reverses the use of the limbs in ordinary locomotion; there the thrusting is done by the fore-legs, and the weight of the falling body is received on the hind; in the jump the hind-legs do the thrusting and the fore-legs receive the weight of the falling body.

In **Kicking** with both hind-legs (Fig. 214) the head is depressed, a powerful contraction of the muscles of the quarters and back, A A, throws the croup upwards, the hips are flexed through B B, the stifles by the contraction of C C, and both legs are violently extended through D D. No estimate of the force employed in kicking can be made. A shell is not productive of more damage than that caused by a determined kicker. It is no figurative

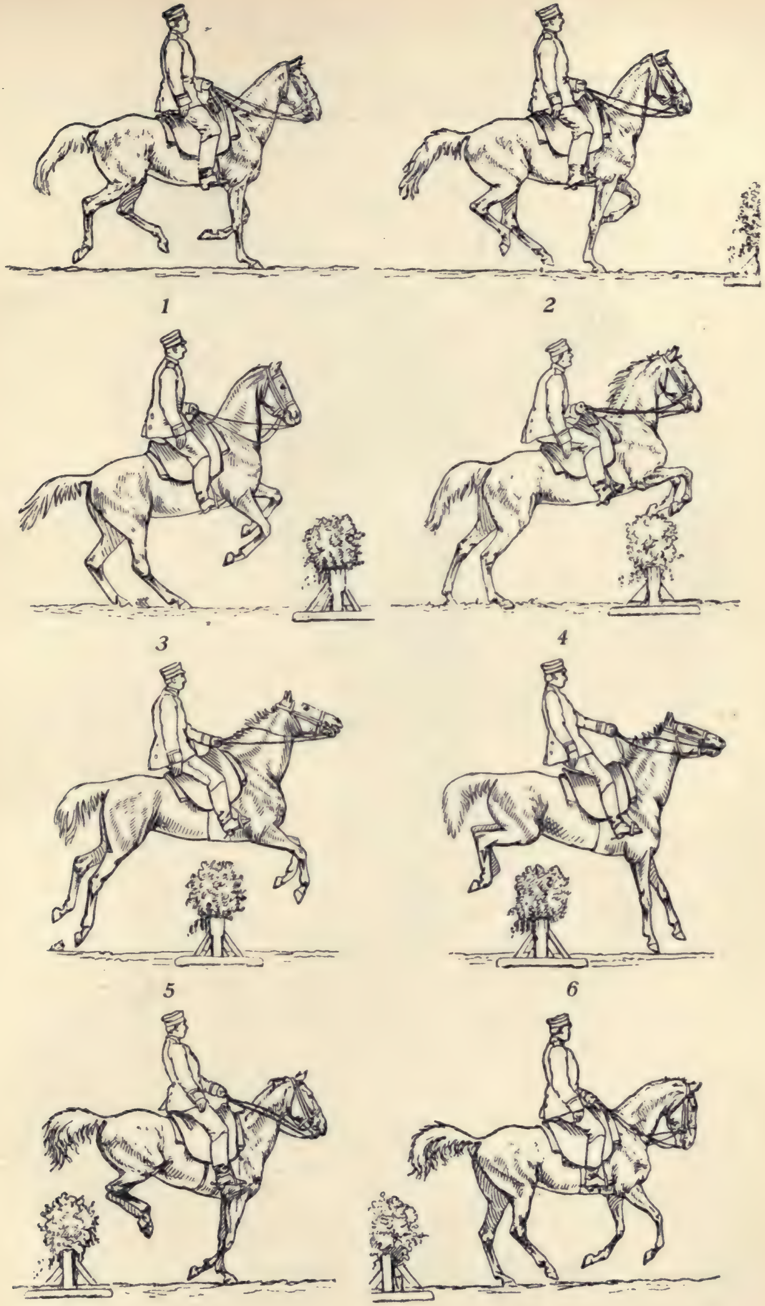

FIG. 213.—THE PHASES OF THE JUMP (ANSCHÜTZ)

expression to say that under suitable conditions the muscles may be heard to contract. Kicking may be practised either

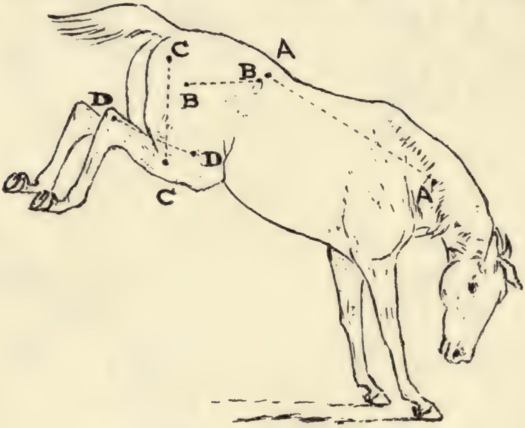

Fig. 214.—Kicking (after Peyremol).

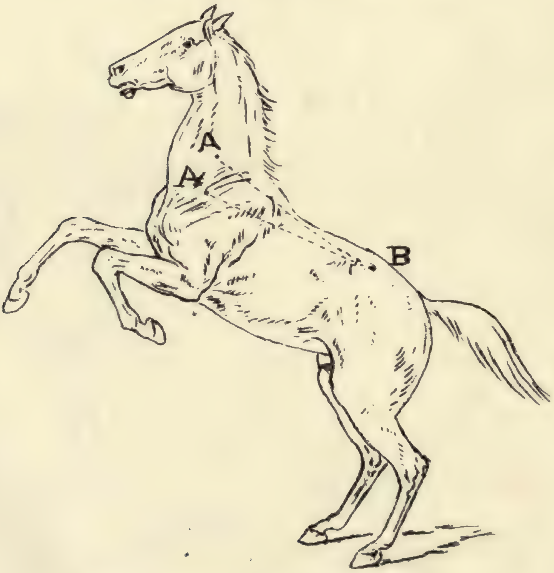

Fig. 215.—Rearing (after Peyremol).

with one hind-leg backwards, forwards, or outwards. The two latter are very dangerous; fortunately, few horses can effect them. Owing to the presence of the pubo-femoral liga-

1 and 8, *ilium*; 4, spinous processes of dorsal vertebræ; 2, 3, 5, and 6, *Longissimus dorsi*, 6 being the portion known as the *semispinalis*, 7, *Ligamentum nuchæ*; 9, *transversalis costarum*.

The longissimus dorsi is the largest and longest muscle in the body. When the head is raised, it acts from behind forwards, and pulls the neck and body farther back as in rearing. When the head is depressed, it acts from before backwards, and raises the croup and loins as in the act of kicking (Fig. 214). In consequence, if a horse's head is kept raised, he cannot kick with both hind-limbs.

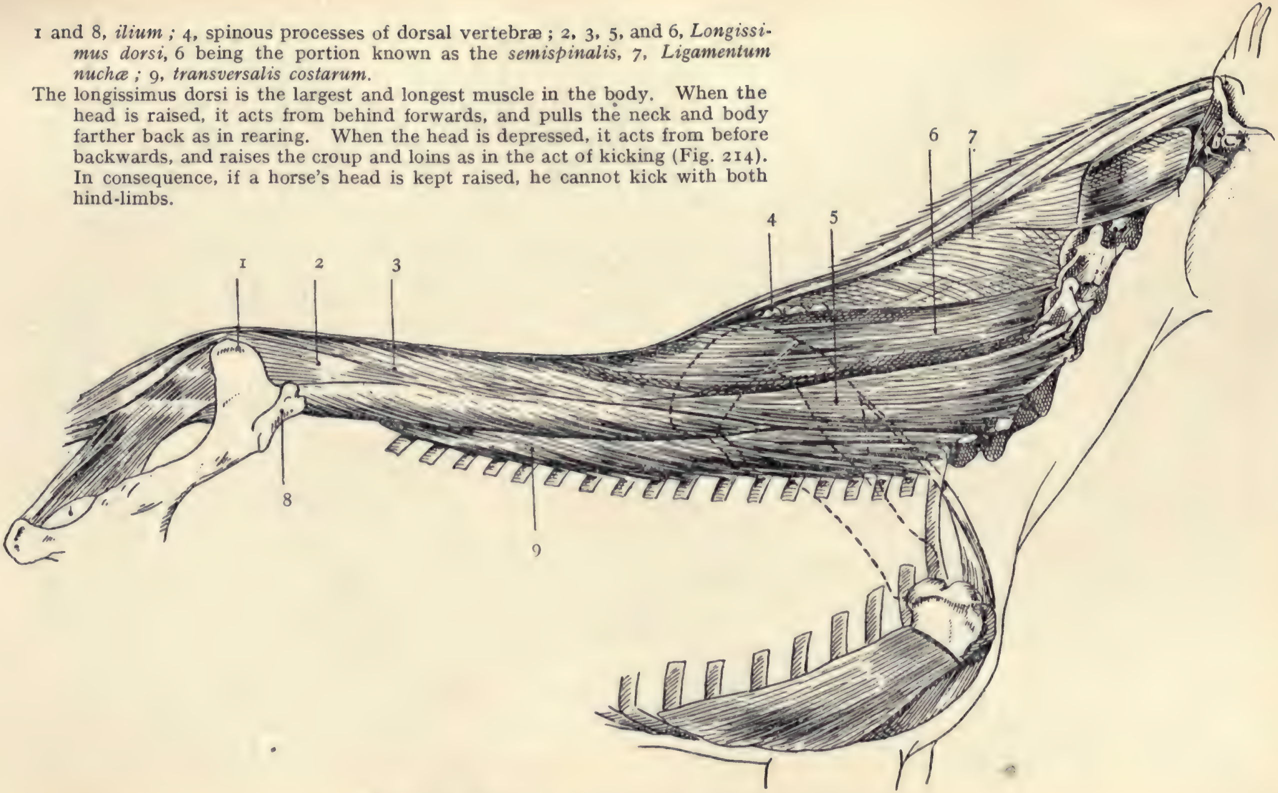

FIG. 216.—MUSCLES OF THE BACK AND LOINS (ARMSTEAD).

ment, a horse can only kick outwards with difficulty. It is known as 'cow-kicking,' but this term may also be applied to the forward kick. Striking with the fore-feet and cow-kicking are not common among nor characteristic of British horses; they are methods of attack particularly employed against man.

It is rather remarkable, however, that our horses should be so much more given to kicking among themselves than those of Continental nations.

In **Rearing** (Fig. 215), the fore-hand is raised by the centre of gravity being thrown back, the body pushed upwards by the fore-limbs, and at the same time raised by a contraction of the long muscles of the back (A B) which run from croup to neck, attached throughout their whole length to the vertebræ (Fig. 216). The muscles of the hind-limbs keep the stifle-joint closed, and the hock-joint open, without which the extra weight would cause the animal to sit down. The position in Fig. 215 is one of perfect stability. More powerful contractions of the muscles inserted into the cervical vertebræ will pull the body farther back, and if it passes outside the base formed by the hind-feet, the animal comes completely over, either on to its side, or frequently on to the occiput when rearing through temper.

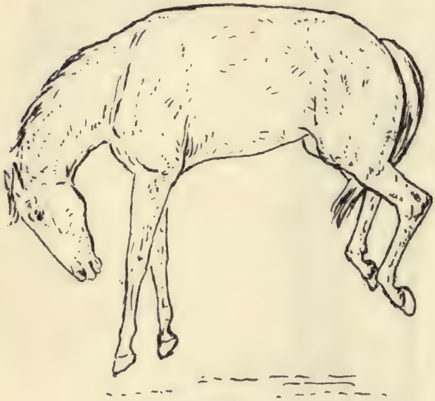

FIG. 217.—BUCK-JUMPING (AFTER PEYREMOL).

In **Buck-jumping** (Fig. 217) the animal springs bodily and suddenly off the ground, the head being depressed between the fore-legs and the back violently arched. In this action the psoas muscles play an important part by bending the hind-quarters inwards, but they cannot by themselves produce the arched condition of spine, which largely depends, apart from the upward spring, upon the ability to get the head down, the neck bent, and the abdominal muscles firmly contracted. Much the same configuration of spine occurs when horses are cast for operation, and in practice this is controlled by keeping the head and neck straight, and the tail from being forcibly drawn in. In buck-jumping it is the spring which displaces the rider.

SECTION 3.

Work.

The **Amount of Work** expected from horses is a question which has hitherto been greatly lacking in exact expression. That many animals are worked beyond their powers is undoubted, the evidence being the short period of their useful life. In days gone by, when the horse was the only means of transport, there was no attempt made to save him, especially in public vehicles; his life in the early stage-coach was three years. The stages were from fourteen to twenty miles in length, but experience and economy brought them down to ten miles. Youatt[*] tells us that towards the end of the eighteenth century, during election-time, bets were made as to which express would kill the greatest number of horses.[†] In his day animals in the public omnibuses only lasted five or six months. Taplin, writing in 1793, says that the rage for expeditious travelling was leading to the destruction of thousands of horses. In an otherwise admirable book on horse management, published in 1805,[‡] it is stated that a horse should travel thirty to forty miles on end without drawing rein at from eight to ten miles an hour; this is described as ordinary work. Severe or, as it is termed, 'extraordinary' work was represented by a gallop of twenty miles, or trotting sixteen miles in the hour. W. Ward,[§] in 1776, advised that a distance of forty-five to fifty miles a day in three stages should not be exceeded. He says he knew of people doing sixty, seventy, and eighty miles a day, but it required a very good horse, and could *only* be done for one or two days. J. Lawrence, writing in 1809,[‖] considered that fifty to sixty miles a day, between 7 a.m. and 5 p.m., could be done in stages of twenty miles, trotting and cantering alternately. In a journey of weeks and months together, he regarded twenty to thirty-five miles a day as suitable. The ordinary hack of that period is described as travelling forty or fifty miles a day at seven or eight miles an hour, and it is stated that with a suitable weight they may do this for two or three successive days. The best hack did ten or eleven miles an hour, and anything over sixty miles a day was considered 'a severe trespass on their powers.' These facts are mentioned in order to explain that the general feeling during the eighteenth century was in the direction of excessive work, the racing especially being of a most punishing character. When Watt, who presumably knew nothing of horses, was determining the working power of his engine, he adopted a standard known as 'horse power,' which has ever since been misleading. He found that a horse could raise a weight of 150 pounds passed over a pulley at a rate of 220 feet a minute (equal to 2½ miles an hour) : 150 × 220 = 33,000 pounds lifted 1 foot high per minute, or 33,000 foot-pounds per minute. From that time, on the basis of Watt's original excessive estimate, the most extravagant demands have been made on the strength of horses, for which engineers and mathematicians, who alone have studied the question, have been responsible. A horse can, of course, raise 150 pounds at the velocity mentioned, but the practical question is for how long ? He could do it for three and a half hours and not be overworked, but eight actual working hours are expected from him, and the standard then becomes excessive. Horses ploughing frequently exercise a force of 150 pounds, but here the pace is the saving factor.

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[*] 'The Obligation and Extent of Humanity to Brutes,' 1839.

[†] In the *Gentleman's Magazine* for 1825 it is stated that a stage-coachman admitted to having killed fifty horses in one year from overdriving.

[‡] 'Analysis of Horsemanship,' Adams.

[§] A 'New Treatise on the Method of Breeding, Breaking, and Training Horses.'

[‖] 'History and Delineation of the Horse.'

Mechanical daily work is the product of three quantities—the *effort*, the *rate*, and the *number of working hours*. The difficulty lies in determining the effort ; there is no means of ascertaining this with any degree of precision in riding-horses, but with draught animals the introduction of a dynamometer registers it with sufficient accuracy. It is evident, however, that the force of traction varies with the character of the roads, and in practice it is found that even on a fairly level surface it varies from moment to moment, depending upon the size of the obstruction or the nature of the irregularities met with by the wheels. There are many other features, apart from the nature of the road, which influence the question of effort in draught—for instance, the height of the wheels, the width of the tyre, the presence or absence of springs. These points are only referred to ; they belong to the realm of mechanics, but their physiological bearing in increasing or reducing the effort required is well known. Experience goes to show that eight hours' work at a walking pace of three miles per hour, with a load drawn without difficulty though with effort, constitutes a working day. If the load or pace be increased, the period of labour must be reduced.

The amount of work performed is spoken of as *foot-tons* or *kilogrammeters*—viz., so many tons raised 1 foot or so many kilogrammes raised 1 meter. The published tables of work by Redtenbacher, Rankine, Morin, etc., are all too high. These place the normal daily work of a horse at from 6,200 to 6,700 foot-tons (1,926,544 to 2,071,104 kilogrammeters). Kellner and Wolff, in their experiments on nutrition in horses caused 2,154,000 kilogrammeters of work (7,000 foot-tons) to be performed daily on a circular dynamometer,* but the writer believes that the following more closely approximates to what should be demanded for regular daily work :

A moderate day's work = 3,000 foot-tons.
A hard day's work = 4,000 foot-tons.
A severe day's work = 5,000 foot-tons.

As a means of conveying to the mind the value of quantities which cannot be visualised, the work in the following table is equivalent to 3,000 foot-tons, it being assumed that the weight of the animal, in addition to the weight carried, is equal to 1,000 pounds :

Walking at	3	miles per	hour for	8·7	hours.
,,	4	,,	,,	5·3	,,
,,	5	,,	,,	3·7	,,
Trotting	8	,,	,,	1·5	,,
Cantering	11	,,	,,	1·0	,,

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* This is the amount Watt's horse would have performed in eight hours.

The calculation of the daily work performed by horses, either in saddle or draught, can only be roughly approximate. The following formula gives the result in foot-tons for saddle-horses:

$$\frac{(W+W^1)\times D}{F\times 2240};$$

where W is the weight of the horse;
W^1 the weight carried in pounds;
D the distance travelled in feet;
F the co-efficient of resistance;
2240 the number of pounds in a ton.

For the purpose of ascertaining the energy expended in draught, it is necessary to know the force of traction. This is a variable quantity depending on the load and the nature of the road; but the dynamometer gives it with sufficient approximation. The formula then becomes—

$$\frac{(W+W^1)\times D}{F\times 2240}+\frac{T\times D}{2240}.$$

The first part of the formula remains as before, in the second half—

T = the force of traction in pounds.
D = the distance travelled in feet.
2240 = the number of pounds in a ton.

As a guide to the force of traction, the following results have been obtained by experiments with vehicles on a level road:

	Force of Traction per Ton.
Smooth surface	31 lbs.
Paved	45 ,,
Macadam	44 to 67 lbs.
Gravel	150 lbs.
On arable land	200 ,,

It must not be forgotten that in addition to the effort required to carry or drag a load, there is another source of expenditure—*i.e.*, the force required to move the animal's own body. Many observations have been made by Zuntz and Lehmann to ascertain what this amounts to on the basis of the oxygen absorbed. For a horse weighing 500 kilogrammes (1,100 pounds) they found that the effort necessary to move the body was equal to 22·4 kilogrammeters of work for every meter (3 feet 3 inches) travelled.* That is to say, the resistance the body offers to being moved is overcome by a force of 50 pounds for every foot of ground passed over. Fifty pounds are $\frac{1}{22}$ of the animal's body weight. This number is known as the co-efficient of resistance. The value of the co-efficient depends upon the pace—the higher the velocity, the greater the resistance—and, in consequence, a greater effort is required to transport the body. In man the co-efficient of resistance at three miles an hour is $\frac{1}{20{\cdot}59}$, at four miles an hour $\frac{1}{16{\cdot}74}$, from which it would appear that the horse moves his body weight with less effort than does a man. The co-efficients for the higher velocities in the horse have not been ascertained. In the following table those for man are given from the calculation made by the Rev. Professor Haughton. They are probably near enough for our purpose, which is to illustrate the fact that the body weight of an animal forms no inconsiderable part of its load, and that the effort to move it increases with the velocity :

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* *Experimental Station Record*, Agricultural Department, U.S.A., vol. vii., No. 7, 1895.

Velocity in Miles per Hour.	Co-efficient of Resistance.	Velocity in Miles per Hour.	Co-efficient of Resistance.
3	$\frac{1}{20{\cdot}59}$	7	$\frac{1}{10{\cdot}72}$
4	$\frac{1}{16{\cdot}74}$	8	$\frac{1}{9{\cdot}60}$
5	$\frac{1}{14{\cdot}10}$	9	$\frac{1}{8{\cdot}68}$
6	$\frac{1}{12{\cdot}18}$	10	$\frac{1}{7{\cdot}52}$

It is a very difficult matter to obtain exact information regarding the work performed by horses. Fortunately, a good deal of precise information was collected many years ago in connection with the wear and tear of animals, at a time when road-building in this country was being scientifically studied, and still later when the running of coaches had, in consequence of the improvements in the roads and the general improvement in the care and management of horses, become an art of national importance. Information was thus obtained of the force of traction over different gradients, and the amount of work expected from the horses. The following table is by Stewart ;* it shows the daily distance travelled, the velocities, the weight of the load, and number of working hours :

CARRIERS (TWO WHEELS).

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Hours Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
2¾	22	26	13	8	6	132
3	27	34	17	9	4	108

In the last observation it will be observed that the increase in pace, in distance travelled, and in load, lead to a reduction in the number of working days.

WAGGONS (FOUR WHEELS).

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Hours Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
2	22	60	30	11	6	132
4	22	40	20	5½	6	132

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* 'Stable Economy,' 1840.

In the second observation the pace is increased, the load reduced, and the working hours diminished by half.

STAGE-COACH.

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Hours Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
8	16	32	16	2	5	80
9	16	46	11·5	1¾	3	48

MAIL-COACH.

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Minutes Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
9½	9	35	8·7	57	7	63
10	8½	30	7·5	51	7	59½
11	8	30	7·5	44	7	56

In the above table a small increase in pace necessitates a reduction in the load and distance travelled, and the duration of the period of work.

The draught employed in the stage-coach in the example given was 62½ pounds per horse on the level, which in the mail-coach was reduced to 40 pounds per horse. It is manifest that with all increase in velocity something must yield—either the effort must be reduced or the duration of labour, or both. It has been shown by actual experiment what amount of increased effort is required to pull a definite weight (1 ton) on a good road at varying velocities and on different gradients.* In the following table only one gradient is taken for the purpose of illustration :

	Four Miles an Hour.	Six Miles an Hour.	Eight Miles an Hour.	Ten Miles an Hour.
	Lbs.	Lbs.	Lbs.	Lbs.
Level	76	80	85	91
1 in 64	109	115	120	126

This shows the increase in force required, even on a good road, for every increase of velocity, and the extra effort needed where a load has not only to be drawn but lifted through a height, as it is in the case of uphill work.

The Physiology of Draught.—The horse, with its horizontal spine, was never intended to carry weight; its muscular power is best exerted in hauling, owing to the size of the base on which the animal stands and the immense weight which can be thrown forward beyond the base. The horse in draught allows his weight to act as a falling body, but it would be of no mechanical value if it fell vertically; it has to fall obliquely, and to secure this the feet are employed as a means of purchase, while the body is kept on the move.

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* 'A Treatise on Roads,' Parnell, 1838.

In ordinary draught-work simple pressure against the collar suffices to move the load, but where the latter is considerable the animal gets closer to the ground, bending both knees and hocks in order to obtain a foothold, and pressing forward from the hind-feet especially on starting. In starting a heavy load the diaphragm is fixed, the abdominal muscles tense, those of the hind-quarters so shortened that the skin over them is thrown into ridges; the muscle tensing the fascia of the thigh stands out like a cord, and if ascending a hill, the toes of the fore-feet are turned in, perhaps in order to increase the size of the chest by turning out the elbows. In heavy draught body weight tells, and with well-made horses body weight and height go together. The increase in body weight for increase in height may generally be considered to be 1 hundredweight for every 4 inches (1 hand); so of two horses, one of 15 and the other of 16 hands, all other things being equal, the latter should be able to exert a force in draught roughly 112 pounds greater than the other. Neither height nor weight govern the indefinable quality of spirit and determination. Of two horses of equal weight and similar build, one may be invaluable, the other worthless, as a worker.

The strain in heavy draught is not confined to the limbs; it is impossible for a horse to start a weight unless the muscles of the back and loins are fit, and it is equally impossible for him to stop it unless these parts are in sound working order. In heavy draught-work on the level it may sometimes be noticed that the toes of the fore-feet are the first to make contact with the ground. This is due to the animal being unable to extend his shoulders properly owing to the load. Though the horse is designed to drag weight, he only drags it well on a level. Uphill his power rapidly diminishes, owing to the effort required to carry his own body weight. If, for example, he hauls one ton on the level with an expenditure of 60 pounds, he will require to exert a force of 223 pounds to ascend a hill of 1 in 14, and this increase is made up of 156 pounds for the load, and 67 pounds to counteract the gravity of his own body weight. So badly, indeed, does a horse climb a hill with a load, that Desaguliers* stated that, if the hill be steep, three men, each carrying 100 pounds, will ascend it faster than a horse dragging 300 pounds. Telford showed that, where possible, 1 in 40 should be the maximum inclination of the road; anything over that greatly increased the work of the horses. One in forty is the *angle of repose*—viz., the steepest acclivity down which a vehicle will not roll of its own gravity.

Strength of Horses.—A comparison between the strength of a horse and that of a man has frequently been made, and the amount variously stated at from five to seven men. We have found that most horses weighing about ½ ton will just pull seven men along, but in the case of a notoriously powerful draught-horse, weighing 14 hundredweight, his strength was equal to thirteen men, whom he dragged very slowly along. This, however, is most exceptional. The greatest force a horse can exert for a few seconds in a steady pull is known as the limit of his strength ; no horse can possibly exert in draught a force equal to that of his own body weight. The writer tested the question on the dynamometer, and found that horses pulled, according to their spirit, from 65 to 78 per cent. of the body-weight.* The grouping obtained was as follows :

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* 'A Course of Experimental Philosophy,' 1763.

Excellent pullers,	78·5	per cent.	of their	body weight.
Good ,,	77·6	,,	,,	,,
Fair ,,	70·6	,,	,,	,,
Bad ,,	65·6	,,	,,	,,

The only horse he met with which pulled 88 per cent. of his own body weight was the animal mentioned above as moving thirteen men.

The **Weight a Horse should Draw** is a question frequently asked. Other things being equal, an animal's power of traction varies directly as his body weight. Working on these lines, an attempt has been made by the writer to ascertain, in the regular draught-work performed generally throughout the country, what proportion the total load bears to the horse's body weight. In this way it is hoped data have been obtained which will enable the question of overloading to be dealt with on a sound basis.

The mean of 650 observations in England was that the horse dragged a load equivalent to 2·53 times his body weight. From the nature of the inquiry it was impossible to avoid favourable cases being selected, but subsequent investigations, where this was specially avoided, show that for work outside towns and cities this ratio may be accepted.† In cities, where the roads are good and friction reduced to a minimum, the ratio of load to body weight may be raised to 1 to 3·5. In Lancashire the mean ratio is 1 to 3·5, but in individual cases it may be much higher, even 1 to 5·5. These represent heavy loads pulled short distances by specially heavy horses and for a small number of hours only, whereas the ratio of 3·5 represents eight working hours a day on good roads, though moderately hilly.

Seventy years ago Stewart put the load for slow draught at 22 to 30 hundredweight, cart included. A large contractor at Manchester, in his evidence before the Strathnairn Committee forty years ago, stated that nothing beyond 25 hundredweight for ordinary draught-work (exclusive of the cart) should be placed behind any horse, no matter whether the roads be good or bad. This is in the ratio of 1 to 3·4, and supports the correctness of this proportion. For light draught a load of 15 hundredweight, and for heavy draught one of from 20 to 25 hundredweight, in both cases exclusive of the vehicle, appears to be an average amount. The vehicles are heavy, one of two wheels weighs from 7 to 11 hundredweight, while a four wheel waggon weighs about 15 to 16 hundredweight.

The following tables present a physiological statement of the question of draught for an ordinary working day of eight hours :

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* 'The Maximum Muscular Effort of the Horse,' *Journal of Physiology*, vol. xix., 1896.

† The writer is indebted to Mr. Mattinson, F.R.C.V.S., A.V.C.(S.R.), and Captain W. L. Harrison, F.R.C.V.S., A.V.C. (T.F.), for several observations and much valuable information.

ROADS OUTSIDE CITIES AND TOWNS.

		Ratio of Body Weight to Load.
Walking pace		1 to 2·5
Trotting	two wheels	1 to 2·0
	four wheels	1 to 2·3

ROADS IN CITIES AND TOWNS.

		Ratio of Body Weight to Load.
Walking pace		1 to 3·5
Trotting	two wheels	1 to 2·2
	four wheels	1 to 2·5

For loads in excess of the above, the hours of labour must be reduced, and horses of sufficient substance employed :

				Minimum Body Weight of Horse.
Where the ratio exceeds	3·5,	but does not exceed	4·0	15 cwt. 0 qrs.
„ „ „	4·0	„ „	4·5	16 „ 0 „
„ „ „	4·5	„ „	5·0	16 „ 2 „
„ „ „	5·0	„ „	5·5	17 „ 2 „

For as long as observations on draught have been made, the fact has been noted that two horses working side by side do not pull the sum of their individual efforts. This has been attributed to such causes as not working in exact rhythm, and, if in teams, to loss arising from being too far from their work. These are the chief sources of loss, but there is another, not, perhaps, so obvious. Horses are very human in some of their failings, and one is an inclination in double harness or in team not to take their full share. The question cannot be further considered here, but carriers and contractors have a special scale for pairs and teams, which is less than what each individual horse is capable of drawing.

Weight a Horse should Carry.—This question is one especially affecting the vital interests of mounted troops ; there is a great difference between the total weight and the *effective* weight an animal can carry. As in the case of draught, the question of weight is largely influenced by that of pace. Generally speaking, the weight an animal can carry bears some proportion to its own body weight, but this rule appears not to apply to the diminutive breeds of horses. The Burmese pony carries a soldier in campaign kit whose feet are within a few inches of the ground. A Korean pony does his thirty miles a day in a roadless hilly country, carrying 160 to 200 pounds. It was stated in 1807* that a Shetland pony would carry a 12-stone man forty miles in one day with ease. Lawrence, in 1810,† stated there was a country postman, working between Glasgow and Edinburgh and riding 16 stone, who carried his ' northern pony ' in his arms to avoid paying toll. The South African farmer, standing over 6 feet in height, rides a lightly-built pony remarkable distances, either at a canter or walk. Our own Exmoor and Dartmoor ponies afford similar instances of endurance. Facts somewhat similar to these suggest that as the horse became bigger his spine became less fit to carry weight. At no time is a horizontal spine a weight-bearer. In proportion to his weight a man can carry far more than an ordinary horse, for the reason that he carries it on a vertical spine. The nations which carry the heaviest weights carry them on their heads, and no doubt a horse could carry more if it could be placed over his hip-joints, where, in fact, the man sits who rides a donkey about twice heavier than himself. The weight carried by pack-horses, at the time when these furnished the only means of communication in this island, was from 16 to 19 stones (102 to 121 kilogrammes) at their own pace. Desaguliers* said that in his day (1763) the pack-horses used by the fellmonger and skinner carried heavier weights than any others, and were sometimes loaded with 32 to 40 stones (204 to 254 kilogrammes), carried at a very slow pace. If what we are told respecting the weight-carrying power of the Cleveland pack-horse can be believed, their capabilities exceeded those of any other breed. Culley (1794)† is responsible for the statement that three Cleveland mares each carried 50 stones (318 kilogrammes) sixty miles in twenty-four hours, and did it four times a week. Youatt ‡ states that mill-horses have carried 65 stones (413·6 kilogrammes) two or three miles. A man will carry for long distances a third of his body weight, and for short distances more than his body weight. The Japanese coolie carries 90 pounds, or even 140 pounds, long distances, and no weight seems too great for the Egyptian. The writer has shown that the effective weight a horse in good condition will carry for long distances, lies between the one-sixth to the one-fifth of the animal's own body weight.§ The mean weight of a cavalry horse is 1,100 lbs. (500 kilogrammes), so that the *effective* weight he is capable of carrying may be taken at 14 stones (83·2 kilogrammes). Cavalry horses are called upon to carry as much as 20 stones, or 280 pounds (127·2 kilogrammes), roughly, one-quarter of the body weight, an amount greatly in excess of their strength.

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* ' The Complete Farmer.'

† ' Treatise on Horses.'

Apart from the features touched on above, the main physiological fact connected with weight-carrying in horses is that the muscles of the back and loins must be conditioned for the work. An animal in the hardest condition for draught purposes is quite unfit to carry a man; the muscles of the back and below the loins are unable to carry weight unless the animal is properly conditioned beforehand. And this holds good for any class of work which necessitates the employment of a fresh and unskilled group of muscles.

The Speed of Horses—*The Gallop*.—The fastest pace at which a horse has been known to gallop is at the rate of 37·69 miles an hour. The animal was Salvator, who in 1890 was galloped on a straight course against time. Flying Childers, the fastest horse known in this country, galloped 3¾ miles, at a velocity of 34¼ miles an hour. In another trial, of over 4 miles, the speed attained was an average of 33·62 miles per hour. Flying Childers has been credited with galloping a mile in a minute, but this is impossible. The mean velocity for the Derby during the last ten years has been 33·54 miles per hour, the distance being 1½ miles. For the Lincolnshire Handicap, the distance of which is a mile, the average speed for ten years was 33·84 miles per hour. The ordinary gallop employed varies from 12 to 14 miles an hour. The length of the stride is from 17 to 20 feet for the average horse, for the race-horse considerably more. Flying Childers was credited with a stride of 25 feet.

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* *Op. cit.* † 'Observations on Live Stock.' ‡ 'The Horse.'

§ 'The Weight of a Horse and its Weight-carrying Power,' *Journal of Comparative Pathology and Therapeutics*, vol. xi., No. 4, 1899.

The Canter varies greatly in velocity, depending, as we have seen, on the length of the spring. The stride may be from 9½ feet in a slow, to 11½ feet in a fast, canter.

The Trot is generally performed at a pace of 7½ to 8½ miles per hour, the length of the stride being between 7 and 10 feet. When trotting matches were popular in this country, some remarkable feats of endurance were obtained. In 1780* a mare trotted 16 miles in 58½ minutes, carrying 12 stone. She repeated the performance when eighteen years old. In 1785 Archer trotted 16 miles in 54½ minutes, but died the next day. In America, where trotting has reached a degree of excellence unknown elsewhere, some astonishing velocities have been obtained, the mile being covered in 1 minute 58½ seconds, or 30·4 miles per hour.

The Walk of an ordinary horse is a mile every 15 minutes, the length of the stride being from 5 feet 5 inches to 5 feet 10 inches.

Endurance Tests.—A few years ago long rides were inaugurated on the Continent with the object, it was stated, of encouraging the development of the horse for long distance work in war. These rides are practically physiological experiments, and are consequently of interest. The first was from Brussels to Ostend, a distance of 82 miles. The winner covered the distance in seven hours. Of 61 horses entering, 17 died, and 17 got no farther than the sixty-second mile. In subsequent rides the principle of racing was abolished, and the essential factors governing the results were the maintenance of condition and fitness. Two of these may be briefly referred to. One year the distance was 250 miles. This was covered in 50 hours, the last 53 miles being completed at 12½ miles an hour. Another year the distance was 93 miles, which was covered in 10½ hours. Out of 47 starters only 24 came in, and but 15 of these were qualified. Tests such as these are no indication of the endurance of the average horse, for in all these trials the animals are the pick of many thousands, and, notwithstanding, we have seen that 50 per cent. fell out in the last trial above recorded.

Two features in these tests need noting. One of these is represented by an aphorism as old as horses themselves. It is the physiological truth that 'it is the pace which kills.' The other raises the question of whether there is any deterioration in the stamina of horses. Are they as capable of withstanding fatigue as the horse of, say, two hundred years ago? A good deal of evidence might be brought forward, including that mentioned on p. 641, to show that the same powers of endurance are not exhibited, and the explanation would appear to be that with an increase in body height there is a falling off in stamina. The standard of height with horses generally has been raised, in order to obtain greater speed in the case of the race-horses, and with other breeds to meet the demands of fashion. But with this increase in stature there certainly appears to be a reduction in stamina. The cavalry of Frederick the Great astonished Europe, and what they did constitutes an object-lesson for cavalry for all time. But in order to get his results the same class of horse must be employed. The standard of height for cavalry since his day has been raised 4 inches and over.

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* J. Lawrence, *op. cit.*

CHAPTER XVII

THE FOOT

Horns, nails, claws, and hoofs represent a modified form of epithelium, and the surface from which these are secreted corresponds to the deep layers of the skin. The other horny structures found connected with the skin of the horse—*i.e.*, the chestnuts and ergots—have a similar origin. Considered by itself, a piece of horn, a claw, or nail, would not appear to possess any special physiology; but once the nail surrounds and completely encloses the end of the limb, as it does in the ungulata, a special physiology arises, and this reaches its highest development in the solid-footed horse. The foot in this animal has become a highly specialised structure, for the purpose of resisting wear and tear, for supporting the weight of the body, and in saving the foot and limb from concussion. If it were merely a block of horn on which the horse stood, it would offer nothing of special interest.

A foot consists of three feet, each enclosed within the other. Externally there is the hoof or horn-foot; within this is a complete counterpart in fibrous and vascular tissue known as the sensitive foot, and the latter is moulded upon a bony structure which in appearance resembles a miniature foot. It is usual, however, to regard the foot as being divided into two portions, an insensitive and sensitive, or an external and internal, the latter term comprising both the vascular and the bony foot. The internal and external feet are an exact counterpart of each other, the former being on a smaller scale, to enable it to fit into the external foot in the same way as a finger fits into a glove.

The external and internal feet are not independent of each other—one is the complement of the other. The external does not produce itself; it is dependent entirely on the internal for every horn cell it possesses. The internal foot cannot tolerate pressure, not even touch; it is dependent on the external foot, for the circumstance that, in spite of its highly sensitive nature, it is throughout the life of the animal enabled to be kept within ¾ to ½ inch of the ground without causing pain. Growth and protection are not the only features in the foot. No one can listen to the thuds of the galloping horse, or the clatter of one trotting, without realising that every time the feet come to the ground there must be considerable concussion unless mechanisms exist for its prevention; and no thoughtful person will have any difficulty in realising that the horse's foot represents a remarkably small pedestal for such a bulky body to be carried upon. These are the essential features comprised in the physiology of the horse's foot, and must, from their paramount importance, be considered in detail. In order to elucidate them, it is desirable to glance at some of the structural features of the parts concerned.

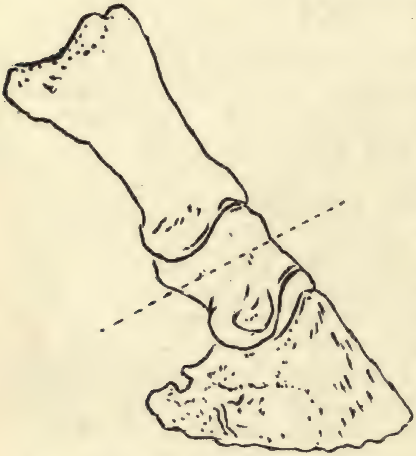

FIG. 218.—PEDAL BONE AND CORONA (MODIFIED FROM LEISERING).

The dotted line through the latter indicates the portion buried within the foot, or hidden by the soft structures at the back.

Bones of the Foot.—The core of the foot consists of bone, around which all the other structures are moulded. The bone is not one solid piece, as might be imagined would be necessary in such a position, but, on the other hand, consists of three pieces. One of these is the pedal bone, which is a miniature foot in shape (Fig. 218), while its substance is porous to such an extent as to resemble pumice-stone in appearance and density. A second bone, the navicular, is very small, of peculiar shape, dense in structure, rests slightly on the pedal bone, and is mainly held in position by ligamentous tissue. The third bone belongs partly to the foot and partly to the limb. One might suppose that the pedal bone should occupy the whole of the interior of the hoof, as high as the coronary edge and as far back as the heels, but this is not so. It only occupies a portion of the internal foot (Fig. 219), mainly situated towards the anterior and lateral parts; the posterior part of the foot contains very little pedal bone, but the deficiency is made up by the introduction of two large plates of cartilage attached to it, over which the structures are reflected and moulded as on the bone itself. This singular deficiency of bone, in a part where one might be led to regard its existence as a necessity, and the presence of large cartilaginous plates to take its place, is due to the lateral movements the foot has to perform, and which could not be carried out if the bone were proportioned relatively to the structure within which it fits. The pedal bone is not placed parallel to the ground, but fits within the hoof, with its toe slightly lower than its heels (see Fig. 219).

The Foot-Joint.—Three bones form the foot-joint (Fig. 220). The question naturally arises why the joint is not composed of two bones instead of three, and what advantage is gained by the introduction of a small dense bone, such as the navicular, into the articulation. The articulation furnished by the pedis is much smaller than that provided by the corona, but by the introduction of the navicular, the pedis plus navicular surface is nearly, but not quite, equal to the corona surface. One use of the navicular bone is to increase the articular surface of the pedis. But it is conceivable that this small articular surface of the pedis might have been increased in some other way than by the introduction of a distinct bone and other complicated apparatus, and it is evident that the value of the navicular articulation does not depend entirely on the fact that it increases the size of the joint, but that it supplies what elsewhere has been spoken of as a yielding articulation (see p. 609). The use of this yielding articulation saves direct concussion. During locomotion, when the foot comes to the ground, the weight through the corona falls in the first instance largely on the navicular, which under its influence yields slightly in a downward direction; from the navicular the weight is transferred almost entirely to the pedis, which also yields slightly under its influence, and in this way direct concussion to the joint is prevented.

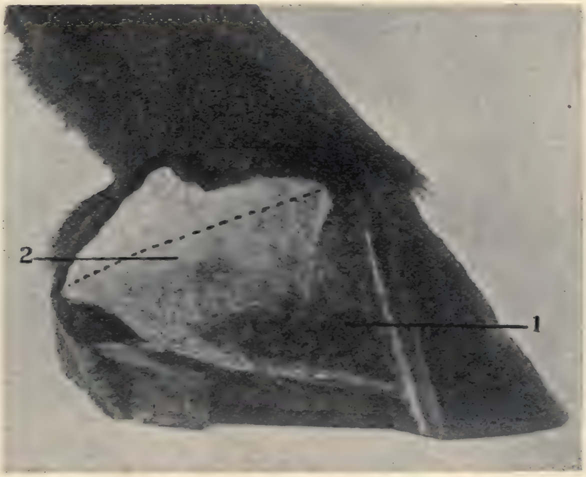

FIG. 219.—THE WALL PARTLY REMOVED IN ORDER TO SHOW THE POSITION OF—(1) THE PEDAL BONE; (2) THE EXTENT OF THE LATERAL CARTILAGE.

The dotted line through the latter indicates the portion within and without the hoof. In the figure the cartilage has curled in and shrunk a little from exposure. It will be noted that the pedal bone is lower in front than behind.

The Navicular Bone and Bursa.—The navicular would be of very little use for the above purpose, if it depended on being kept in position solely by the delicate ligaments which have origin from it.

Its chief support is the broad expansion of the perforans tendon which passes beneath it; between the tendon and the bone the most intimate fitting occurs, and a synovial apparatus exists to save friction. It is probable that the perforans tendon and the inferior face of the navicular are more closely adapted to each other than any articulation in the body, excepting some of those found in the knee and hock joints. Briefly, then, the small dense navicular bone is enabled to form a yielding articulation in the foot, owing to the manner in which it is supported in position by the powerful perforans tendon. It might be urged on purely theoretical grounds that a small bone thus placed in the foot would be very liable to damage, and such is clinically the case. There is no intention here to touch on the subject of navicular disease, excepting in so far as it helps to elucidate the physiology of the part, but it is permissible to regard the lesions of navicular disease in the light of a physiological experiment, and to learn from them how intimately the freedom and elasticity of a horse's action depend upon the navicular bone, and the stilty, pottering, shuffling gait conferred on the animal when this bone is no longer capable of performing its functions properly. The very close support afforded to the navicular by the perforans tendon may possibly be a cause of disease, for the conclusion has been forced on the writer that, under the influence of the weight of the animal, and the counteracting influence of the perforans tendon, the navicular bone must be exposed to considerable compression (see Fig. 220). This compression exists, not only during locomotion, but also during standing. The only complete rest from compression which the navicular bone of the fore-limb obtains is while the animal is lying down. Those of the hind-limbs are relieved from pressure every time the horse rests the leg by flexing the hock,

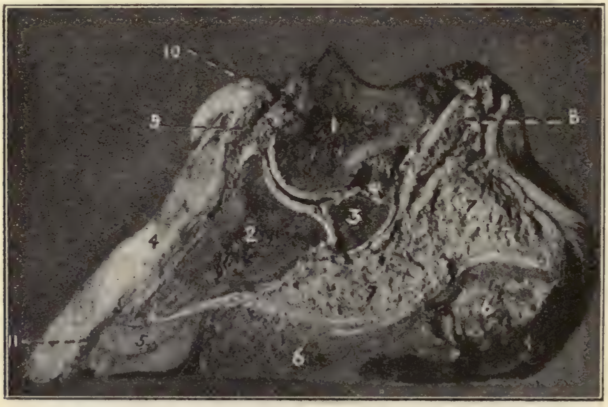

FIG. 220.—LONGITUDINAL SECTION OF THE FOOT.

1, The corona; 2, the pedis; 3, the navicular; 4, the horn wall; 5, the horn sole; 6, 6, the foot-pad; 7, 7, the plantar cushion; 8, the perforans tendon passing under the navicular bone, to be inserted in pedis; 9, the wall-secreting substance; 10, the extensor pedis tendon; 11, junction of wall and sole, the 'white line.'

and no case of navicular disease in the hind-feet has ever been known.

The navicular bone does not exercise any pulley function in connection with the perforans tendon, such as has been usually described—that is, if by the use of the term 'pulley' it is intended to convey the impression that some mechanical advantage is obtained. It is true that by passing beneath the navicular bone the direction of the pull of the tendon is altered, but no mechanical advantage is thereby derived. The perforans tendon at its insertion spreads out fan-shaped, and is attached over a considerable semilunar surface of the pedal bone ; so extensive is this attachment that it is erroneous to believe the tendon plays over the navicular bone. It is a fact that movement occurs between the tendon and the bone, but the tendon is passive, while the yielding of the navicular bone under the influence of the body weight is the active agent. It is interesting to observe the direction in which the largest amount of friction occurs between these two surfaces. Reasoning from the position of the parts, one would think it occurs at the moment the foot comes to the ground ; but if the eroded tendon of navicular disease be examined, it will be observed that the fibres are all stripped *upwards*, and rarely or never downwards. This points to the greatest friction occurring, not when the bone yields under the weight, but when it returns to its place as the body, under the influence of the flexor tendon, passes over the foot. The frequency with which the middle of the ridge of the navicular bone, and the area on either side of it, are affected with disease points to this part as being the seat of the largest amount of pressure.

Lateral Cartilages.—Attached to the heel of each pedal bone is a large curved plate of cartilage, in parts fibrous, in others hyaline in nature. So extensive is this plate that it reaches high above the margin of the hoof—*i.e.*, outside the foot in an upward direction as far forward as the coronet and as far back as the heel (Fig. 219). There is no other structure in the body with which this arrangement can be compared : a bone possessed of two large cartilaginous wings is a something peculiar to the foot. The use of these cartilages is intimately connected with the main principles of the physiology of the foot, to be dealt with later.

Plantar Cushion.—Placed between the two plates of cartilage just spoken of is a large somewhat pyramidal-shaped body known as the plantar cushion (Figs. 220, *7*, *7* ; 221). In appearance it resembles a fibro-fatty mass, composed of interlacing bands, pale yellow in colour, almost destitute of bloodvessels, firm to the touch, yet yielding in its nature.

Mettam* has shown that, though the plantar cushion to the naked eye is fibro-fatty, its microscopical characters show it to be mainly tendinous in structure, the fibres being disposed in bundles running in different directions ; uniting the bundles is a connective tissue, in the meshes of which fat is found in islets, and not abundant, as one of the older names of this body implied.† There is only a small amount of elastic tissue present. The position of the plantar cushion in the foot is at the posterior half, between the cartilages, rising up above the level of the hoof and filling in completely the hollow of the heel. Its inferior face is V-shaped (Fig. 221), and a complete counterpart of the horn-cushion or foot-pad above which it lies. Its position is shown in section in Fig. 220, *7*, *7*, and the manner in which it protects the navicular bursa and tendon. The cushion is softer posteriorly than anteriorly, where at its apex it is dense and fibrous. The cushion does not secrete horn, but its surface is covered by a delicate papillated membrane which secretes the horn of the foot-pad.

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* 'The Development and Histology of the Hoof,' etc., by Professor A. E. Mettam, B.Sc., M.R.C.V.S., *Veterinarian*, 1896.

† Nevertheless, W. C. Spooner, of Southampton, writing in 1840 ('Treatise on Foot and Leg of the Horse'), said analysis showed that the plantar cushion contained no fat in its composition.

Sweat-glands exist in the plantar cushion, situated in and on the side of its central depression. The glands, as figured by Franck, are shown in Fig. 222. A more modern description is given by Mettam. They are large, coiled, single or multiple glands opening on the surface of the horn in the so-called 'cleft' of the frog by means of tubes, which take a very spiral course. They secrete an unctuous fluid, which helps to maintain the horn in a pliable condition.

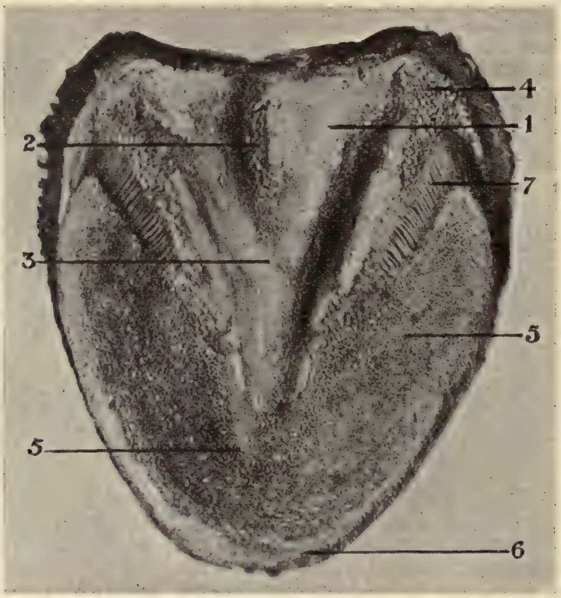

FIG. 221.—THE PLANTAR SURFACE OF THE INTERNAL FOOT.

1, 2, 3, The sensitive foot-pad, or plantar cushion, 1 being the bulbs, 2 the cleft, 4, the termination of the wall-secreting body of the heel, where it blends with the plantar cushion : the numerous papillæ on its surface can be seen ; 5, the vascular or sensitive sole, covered by papillæ ; 6, terminal ends of the sensitive laminæ, which may be seen around the entire rim : it is at this point where each lamina terminates in four or five papillæ ; 7, the laminæ of the wall inflected at the heel, and here forming the sensitive 'bars.'

The **Corium** of the foot completely covers the whole of the pedal bone, plantar cushion, and a large surface of the lateral cartilages. This tissue has received various names—viz., from its colour, the vascular foot; from its appearance, the fleshy; from its character, the velvety foot; whilst from one of its functions it has been termed the horn-secreting foot.

The **Vascular Wall** or **Laminal Tissue** (Figs. 223, *4*; 224, *6*) is composed of corium arranged in the form of a number of leaves lying side by side, which run from the coronet downwards and forwards to the edge of the wall. In number there are about 500 or 600; they invest the entire wall of the pedal bone and the greater part of the lateral cartilages, their extreme vascularity giving the appearance of a thin layer of muscle. The leaves at the toe are longer than those at the heel, where they are very short and turned in under the foot, running forwards beneath it to form the part known as the sensitive bars (Fig. 221, *7*).

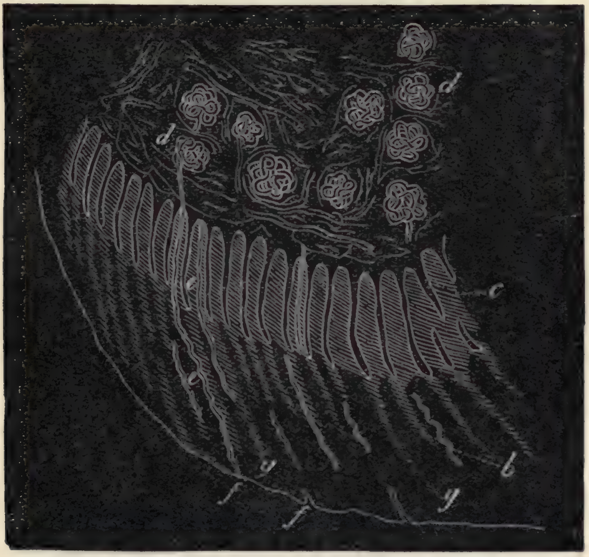

FIG. 222.—THE SWEAT-GLANDS OF THE PLANTAR CUSHION (FRANCK).

d, d, The glands, the corkscrew-like ducts of which (*e, e, b*) pass out through the horn of the foot-pad, opening at *f, f* on to the surface of the foot at the cleft. At *c* is the deep-seated portion of the horn of the foot-pad, where it grows from the papillæ of the corium of the plantar cushion; *g, g* are horn fibres seen in longitudinal section.

If a single leaf, say at the toe, be removed and examined, it is found to commence immediately under the thick cornice-like structure known as the coronary or wall-secreting body, and to be most firmly attached to the pedal bone; in fact, so intimate is the attachment that it is almost impossible to remove this tissue cleanly from the bone. The leaves under the coronet are very short from front to rear (depth), but as they proceed from the coronet towards the ground they rapidly increase in depth, and attain their full depth about ¼ inch or so from their origin. The edge of the leaf is not regular, but denticulated, and at its inferior part each leaf terminates in five or six papillæ. The leaf is extremely vascular—in fact, quite scarlet in colour—the effect over the whole mass of leaves being very striking in appearance. If the tissue be examined microscopically, it is found that part of its substance is devoted to leaf-formation, whilst the remainder is a sublaminal tissue, the function of which is to secure the laminæ firmly to the wall of the pedal bone. This sublaminal tissue has been described by Moeller* as consisting of two layers; the one nearest the bone is designated the *stratum periostale*, and acts as the periosteum of the bone (Fig. 225A, *b*). Outside this is a layer of fibrous connective tissue and elastic fibres, arranged in bundles, crossing and forming networks; this layer is extremely vascular, and has been designated the *stratum vasculosum*. External to this layer are the laminæ, formed of elastic and connective-tissue fibres, as in the previous layer, only the network is much finer. The laminæ contain numerous bloodvessels and nerves.

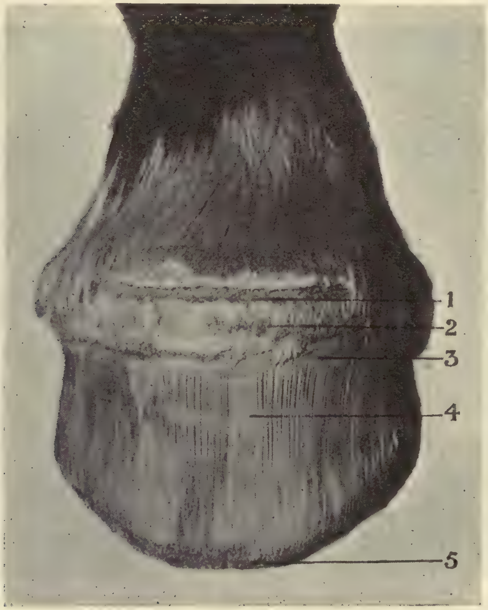

FIG. 223.—THE HOOF REMOVED, AND THE VASCULAR WALL SEEN FROM THE FRONT.

1, Groove between the skin and wall-secreting body from which the *periople* grows; 2, the wall-secreting body: the rough surface is due to papillæ and small adherent fragments of horn; 3, the beginning of the sensitive laminæ; 4, the laminæ; 5, their papillated ends.

The microscopical appearance of a transverse section of the vascular laminæ is shown in Fig. 225A, from Moeller. Each sensitive lamina is not smooth, as its naked-eye appearance indicates, but denticulated, each tooth-like depression representing secondary laminæ, or laminellæ, first fully described by Fleming.* The number of these depends on the depth of the primary lamina, but they may be from 60 to 120 in number. It is quite common to find some of the secondary laminæ bifurcate. The appearance presented on horizontal section is very characteristic, and has been aptly likened by Chauveau to a feather, the barb of which is represented by a lamina and the barbules by the secondary laminæ. The function of the secondary laminæ has been a fruitful source of discussion.

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* *Veterinary Journal*, vol. v., p. 114.

The Origin of the Horn Laminæ.—No one doubts that the wall grows from the coronet, but great controversy has taken place over the origin of the horn laminæ, some saying they grow like the wall from a part of the coronary cushion, and others affirming that they obtain their origin from the sensitive laminæ. If we were to judge solely by the result of pathological processes, we should say the sensitive secreted the horn laminæ ; but Moeller† points out that the sensitive and insensitive laminæ are never in actual contact, and that between them are placed the secondary laminæ of both varieties (Fig. 225B). Therefore he argues that the vascular cannot secrete the horn laminæ, but that the secondary vascular secrete the secondary horn laminæ. If a portion of wall be removed experimentally and the vascular laminæ exposed, in the course of a short time the part becomes covered with a layer of horn, with laminæ on its inner surface, and this has been used as a strong argument in favour of the secretion of horn laminæ from sensitive laminæ ; but the horn which is

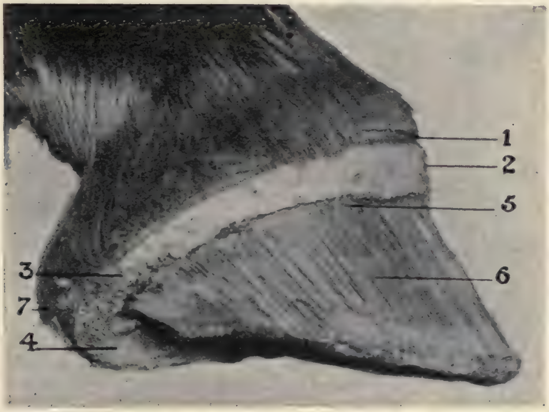

FIG. 224.—THE HOOF REMOVED, AND THE VASCULAR WALL SEEN FROM THE SIDE.

1, The periople groove ; 2 and 3, the wall-secreting body ; 4, the bulb of the plantar cushion, richly covered with papillæ, and running into 3, with which it joins ; 5 and 6, the sensitive laminæ ; 7, increase in size of the periople groove at the heels, where a soft horn is formed, which plasters over the junction of the various foot tissues which here meet. Note that the plantar cushion is below the level of the heel of the pedal bone and lateral cartilage.

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* In 1840 W. C. Spooner, *op. cit.*, wrote : 'The inner edges of the laminæ appear fimbriated, like the edge of a fine-tooth comb.'

† *Op. cit.*

thu secreted is derived from the secondary vascular laminæ, and no one contends that these secrete the primary horn laminæ. The following explanation appears to be the correct one: The horn laminæ are secreted from the lower edge of the coronary body; here protoplasmic cells are poured out between the papillæ; these cells are carried down with the wall, being pressed into and moulded between the sensitive leaves, thus becoming horn laminæ, the exact counterpart in shape of the mould in which they are made. All this occurs in the region marked 3, Fig. 223. As the wall grows down the horn-leaves are carried with it, so that there is a perpetual movement occurring between the slowly travelling insensitive and the fixed vascular laminæ. The rate of this movement is probably about 0·0125 inch in twenty-four hours, on the assumption that the wall grows ⅝ inch in the month. During the

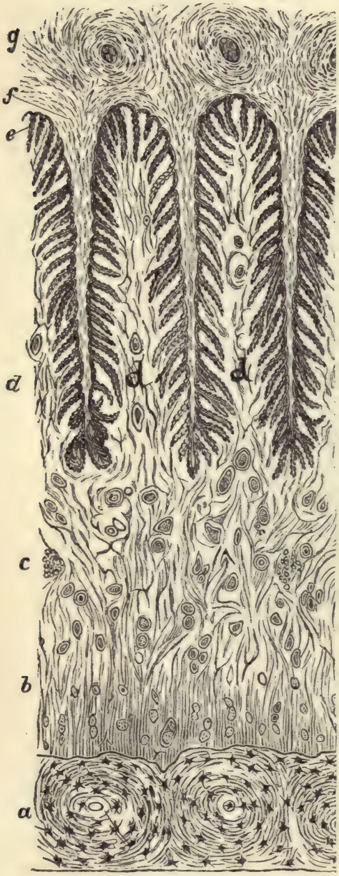

Fig. 225a.—Horizontal Section of the Hoof and Vascular Tissues at the Anterior Part of the Horse's Foot (Moeller).

a, Bony tissue of the os pedis; *b*, stratum periostale; *c*, stratum vasculosum; *d*, sensitive laminæ; *e*, secondary laminæ, or lamellæ; *f*, primary horn laminæ; *g*, wall of the hoof, with its horn fibres.

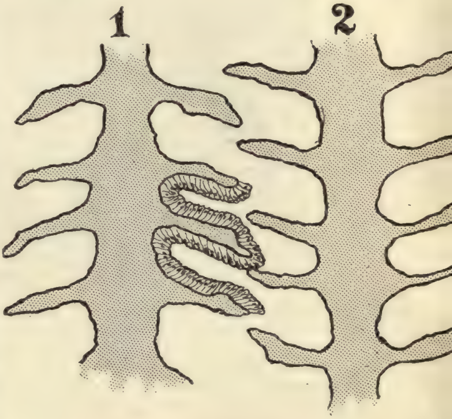

Fig. 225b.—Horizontal Section of Portion of a Pair of Laminæ: (1) Sensitive, (2) Horny, each with their Lamellæ.

The laminæ and lamellæ have been pulled apart; the protoplasmic cells which separate the lamellæ of each type are partly represented. The figure shows that these cells come between both primary and secondary laminæ of each series, which are therefore never in actual contact. It is from these protoplasmic cells that the horn lamellæ are secreted.

time the horny are gliding between the sensitive leaves, the vascular lamellæ furnish them with horny lamellæ; when the wall reaches the sole the horn lamellæ are left behind, while the primary laminæ emerge with the wall destitute of these structures. This statement does not explain away all the difficulties which could be raised, but suffices for practical purposes.

The **Wall-secreting** or **Coronary Body** is a thick, half-round, cornice-shaped welt of material situated above the laminæ (Figs. 223, *2*; 224, *2*, *3*); it has received several names, the most rational being that based on its function as the structure which secretes the hoof wall. Externally this body is covered by a highly vascular membrane possessing long papillæ, which are readily seen by immersing the foot in water, while on section it is fibro-fatty in appearance, and consists of a coarse network of elastic and fibrous tissue. It is this latter which forms the main substance of the welt, which projects like a big rim from the sensitive foot. The basement substance takes no part in the secretion of horn; the papillated membrane which covers it alone carries out this function, while the use of the welt is to provide the secreting membrane with a sufficiently firm and extensive surface. The wall-secreting substance extends all round the coronet from heel to heel, and here joins the plantar cushion. On its superior margin is a narrow groove (Fig. 223, *1*), which is the dividing-line between skin and hoof, and from which a peculiar horn known as the *periople* is secreted. This horn cements over the junction between hair and hoof (Fig. 227, X). On its lower margin the coronary substance fuses with fibres from the vascular laminæ. The entire body fits into a half-round groove in the wall, and the papillæ on its surface are lodged in canals formed in the horn. Beneath the coronary welt is a well-developed subcutis, which unites it to the tissues covering the corona and lateral cartilages. The vascular papillated membrane covering the coronary substance is frequently irregularly pigmented, corresponding to the colour of the horn wall.

The **Vascular Sole** (Fig. 221, *5*) is scarlet in colour, and covered by long papillæ which are lodged in the depressions in the horn sole. In each papilla an artery and one or more veins may be found. The corium covering the plantar cushion is similarly arranged, the papillæ being lodged in canals in the foot-pad, or horn frog.

The **Blood-Supply** to the foot is exceedingly rich. With the exception of the internal organs, there is no part of the body so vascular, and the horse has more blood in his feet than in his brain. Mention has already been made of the scarlet appearance presented by the laminæ, the vascular sole, and the tissue covering the plantar cushion. The pumice-stone-like appearance presented by the pedal bone is for the purpose of affording passage to the innumerable vessels which are passing from the interior of the bone in an outward direction to reach the vascular tissues; in fact, no description or drawing can adequately convey an idea of the appearance presented by this vascular body. The veins are large and numerous (Fig. 226), and are not provided with valves; some pass through the substance of the lateral cartilage, and a large plexus exists both outside and inside the cartilage. The relation of these vessels to the lateral cartilages and the absence of valves are matters which will be considered later.

The **Hoof,** or insensitive foot, is moulded over the sensitive structures in such a way as to cover them completely, and form in horn a perfect counterpart of the sensitive foot. The hoof is composed of a *wall*, with its inflections the *bars*, a *sole*, and a *foot-pad* (frog) ; each of these must be considered separately.

The **Wall** is that part of the hoof which can be seen when the foot is on the ground ; its division into toe, quarters, and heels is for convenience of description, as no natural division exists. On the exterior of the wall, at the meeting of the hair and hoof, is a rim of peculiar non-pigmented horn, previously spoken of as the **peripole**. Under natural conditions, it is grey in colour, soft to the touch, and it cements the skin to the hoof. Its non-pigmented condition is only rendered evident when the foot has been soaked in water or poulticed ; the cells then swell, and a white curdy rim occurs all round the top of the wall (see Fig. 227, X). It is wider at the bulbs of the heel, where it cements over the union not only of skin with foot-pad, but of the meeting-place of the wall and foot-pad (Fig. 224, *1*, *7*).

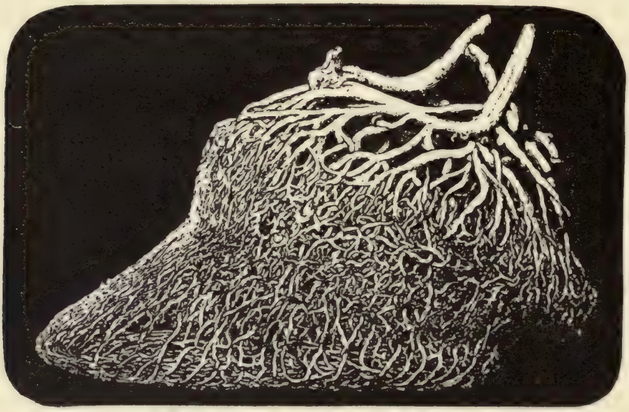

FIG. 226.—THE VENOUS SYSTEM OF THE HORSE'S FOOT (STORCH).

The periople provides the wall with an extremely thin covering, resembling a delicate coat of varnish, which is intended to prevent undue evaporation from the horn beneath.

The **Colour** of the horn of the hoof is commonly described as black or white ; to be strictly accurate, it is neither. The so-called black horn consists of various tints of slate colour ; the white is pale yellow or buff. It is, however, convenient to speak of black and white feet. In dealing with the skin (p. 305), the colour of feet was touched upon, and it was made clear that it depended upon the colour of the hair of the coronet. If this is white, there is no pigment in the skin, and consequently none in the horn ; if it is partly black and white, the foot is striped accordingly. If the coronet is of any other colour than black, the feet are dark ; but if these colours are mixed with white, the feet are striped.* It might be imagined that a grey horse would have white feet, but a grey horse is not a white horse ; and a grey with grey legs has dark feet, but a grey with white legs has white feet. The number of white feet among grey horses is very small.* The physiological importance of non-pigmented horn is its weakness, brittleness, and slow growth, as compared with the pigmented variety. A white foot constitutes local albinism (see p. 304).

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* Colonel Nuthall, A.V.S., informs me that of some 2,500 horses he caused to be inspected, five were recorded to have striped feet with no white on the coronet. This is unusual, and doubtless due to absence of pigment from certain portions of the wall-secreting membrane within the hoof.

The wall is thickest and longest at the toe, thinnest and shortest at the heel. A gradual decrease in thickness occurs from front to rear (Fig. 228) ; but if a section of the wall be made in the direction of its fibres, it will be found that whatever the thickness may be at that particular part, it is maintained from the coronet to the ground surface. The greater thickness of the wall at the toe and quarters as compared with the heels is connected with the wear and tear of the hoof, and the movements which the latter undergoes under the influence of the body weight. If the wall were as thick at the heels as at the toe it would have been a rigid box ; it is, however, a yielding box, and the yielding occurs in the region of the thin wall of the heels. The reason why the wall is thick at the toe is that it is here where the greatest friction and strain occurs. The wall at the heels is suddenly inflected (Fig. 228, *5*), running under the foot in a forward direction for a short distance, and forming an acute angle with the wall. This inflected portion of the wall is called the **Bars** (Fig. 228, *6*), and in the gap formed between the two bars is lodged the footpad. Thus the wall is an incomplete circle of horn, the circle being broken at the posterior part of the foot, and the piece

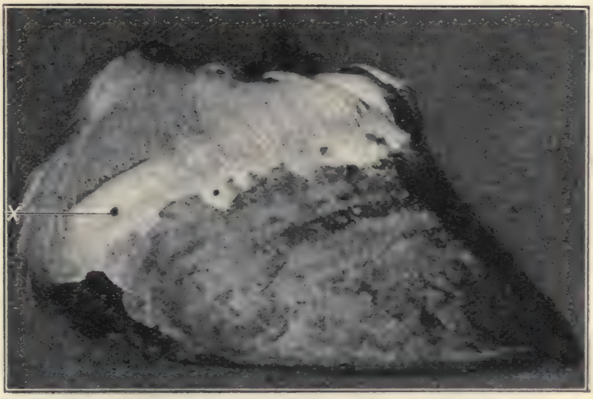


FIG. 227.—THE EXTERNAL FOOT OR HOOF.

The fibrous appearance of the wall may be seen, also the *periople* marked X ; the hair of the edge of the coronet is clipped away to show this band of white horn, which for the purpose of the photograph was swollen by immersion in water.

* I am indebted to Captain Martin Millar, A.V.C., for exact information respecting 500 grey horses : 57·3 per cent., had black feet, 34 per cent. parti-coloured feet, and 8·7 per cent. white feet. He also observes that a dark spot on a white coronet frequently colours the hoof out of all proportion to its size.

of wall which might have completed the circle is sharply bent on itself and caused to run in practically the opposite direction. When this arrangement is considered, it is easy to see the advantages gained. The foot is not a rigid body, but a yielding one; and it would be difficult to understand how any lateral movement could take place had the wall been a complete circle. From their position the bars afford additional strength as weight-bearers, for they represent the wall carried under the foot; they also prevent any rupture occurring between the wall and foot-pad during the lateral movements of the foot.

The hind-feet differ from the fore in shape, being more upright and narrower. They do less work, for they are only employed in assisting to propel the body in the walk and trot, while, from the natural attitude of the horse at rest (p. 601), they are alternately relieved of weight.

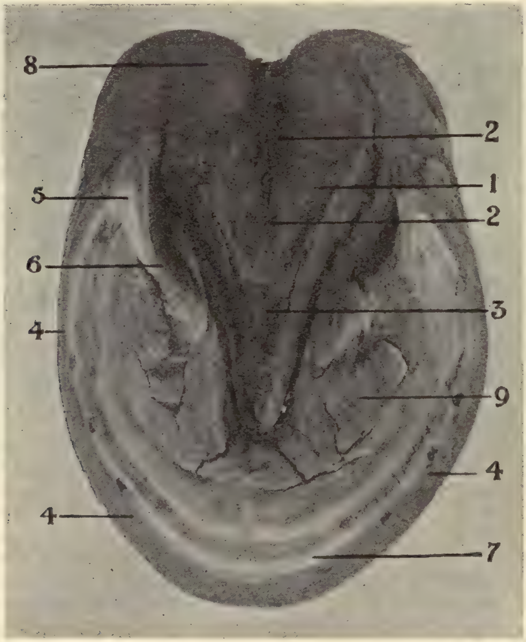


FIG. 228.—THE HOOF SEEN FROM ITS GROUND SURFACE.

1, 2, 3, 8, The foot-pad, 2 being the cleft; 4, the wall; 5, its inflection at the heels to form 6, the 'bars'; 7, the white line; 9, the sole.

On examining the inside of the hoof-wall, a very complex arrangement presents itself. At the upper edge, corresponding to the coronet, is a deep semicircular groove, in which is lodged the thick welt of tissue previously described as the wall-secreting substance. Covering the entire surface of this groove are innumerable pin-point holes, into which the papillæ projecting from the 'substance' are lodged. The thickness of the wall at any one place corresponds to the size of the coronary substance ; the wider it is, the larger the area it affords to the horn-secreting membrane covering it.

Horn Laminæ.—On the inside of the wall of the hoof a number of leaves of horn are found arranged side by side, running all round the foot from heel to heel, and extending from coronet to ground surface. It is easy to see that they correspond in size, direction, and length to the vascular or sensitive laminæ previously described, and, like them, they possess *secondary horn laminæ* or *lamellæ* (Fig. 225B). These insensitive and sensitive laminæ fit into each other by the process of dovetailing, which results in extraordinary strength being obtained. So powerful is the union that, in endeavouring to separate them, the vascular laminæ will often tear from the pedal bone rather than rupture the dovetail. In this way the most intimate and perfect union between the vascular and hoof wall is brought about, and, in addition, other advantages are obtained which will be dealt with shortly. The horn laminæ, as their name implies, are composed of horn, but the secondary laminæ which invest them are composed of cells which are a something between horn and epithelium—*i.e.*, the cells have not undergone a true horny conversion, but remain protoplasmic in nature ; this is recognised by the fact that they readily stain with carmine, whereas horn does not. It will be remembered that though the sensitive and insensitive laminæ dovetail, yet they are never in actual contact, for between them are the lamellæ, both sensitive and insensitive. The sensitive lamellæ look towards the horn wall, the insensitive lamellæ point in the direction of the pedal bone, so that the dovetailing of the lamellæ is not affected at right angles to the primary laminæ (Figs. 225A, 225B). The origin of the horn laminæ has been considered at p. 659.

Horn laminæ are found on the bars, for these, though situated under the foot, are a part of the weight-bearing wall, and possess all its essential structural elements.

The **Sole** of every normal foot is concave (Figs. 229, 230), that of the hind-feet being more concave than the fore. This concavity agrees with the concavity of the solar surface of the pedal bone, which in itself is ample evidence that the general surface of the sole is not intended to bear weight, though the portion in contact with the wall is a weight-bearing surface (Figs. 229, *5* ; 230, *5*). Soles vary in thickness, some being rigid and firm, others thin and yielding ; the sole cannot be too thick. Those shown in Figs. 220, 229, 230, are excellent specimens of a good sole. The growth of the sole is peculiar ; in exactly the same way as was noticed in the wall, the papillæ from the vascular sole fit into pin-point holes in the horn-sole, and horn is developed around them. But here the resemblance ends ; while the horn of the wall is capable of growing to almost any length, until, in fact, it curls like a ram's horn, the horn of the sole can only grow a very short distance before the fibres break off, and scales or flakes of horn are the result ; these either fall out or are pulled out. In other words, the foot determines for itself how thick the sole shall be, and, without any assistance, the fibres break off when the proper thickness has been attained, and allow the part to drop out. This shelling out of the sole, which can be seen in Fig. 228, *9*, is advantageous in the shod foot, inasmuch as the part, not being exposed to friction, cannot wear away. In parts of the foot, such as the wall, which in the unshod foot are exposed to friction, no breaking off of horn fibres occurs ; wear and tear maintain the part at its proper length and thickness. The union between the vascular and insensitive sole is brought about by the papillæ on the surface of the former. The extraordinary length and number of these can only be appreciated by examining the parts under water.

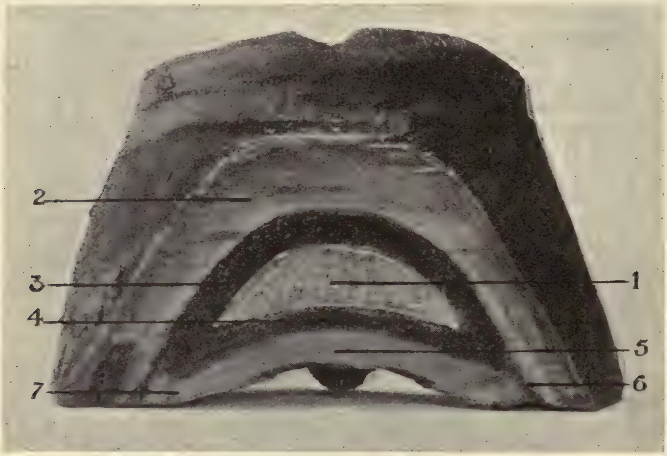


FIG. 229.—A VERTICAL SECTION THROUGH THE FOOT, ONE-QUARTER OF ITS DISTANCE FROM THE TOE TO THE BULBS OF THE HEEL (FIG. 228, *8*).

1, The pedal bone; 2, the horn wall; 3, the sensitive laminæ; 4, the sensitive sole; 5, the horn sole; 6, the junction between wall and sole; 7, the margin of sole capable of bearing weight.

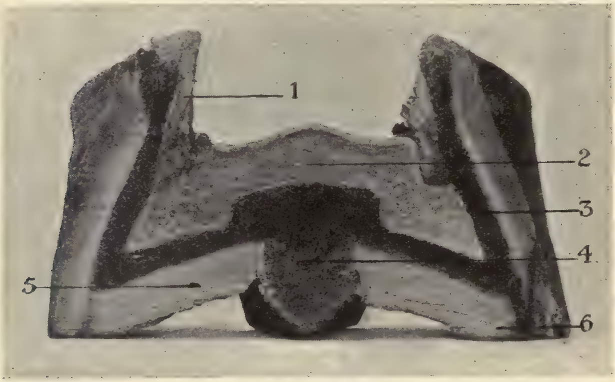


FIG. 230.—A VERTICAL SECTION THROUGH THE FOOT, ONE-HALF THE DISTANCE BETWEEN THE TOE AND THE BULBS OF THE HEEL.

1, The lateral cartilage; 2, the pedal bone; 3, the sensitive laminæ; 4, anterior portion of foot-pad; 5, the sole; 6, the weight-bearing portion of the sole.

The sole and wall are united in a distinctive manner, and the union is indicated by a **white line** (Fig. 228, *7*) which runs around the entire junction of sole and wall. The white line represents the layer of the wall next to the insensitive laminæ (Fig. 231, *6*); within this come the terminal ends of the laminæ themselves, and between these and the sole a layer of much softer yellowish plastic horn (Fig. 229, *6*). This cement substance is secreted by the four or five papillæ found on the end of the sensitive laminæ, shown diagrammatically and microscopically in Fig. 232. The soft cement substance, besides ensuring the union of wall and sole, also admits of slight yielding of the sole, to which reference will be made later. A microscopical examination of the union shows the horn laminæ digitating with the sole between the laminæ, which are now wavy, and no longer in possession of secondary laminæ. The horn is arranged in concentric layers, being formed by the four or five secreting papillæ on the terminal end of the sensitive laminæ.

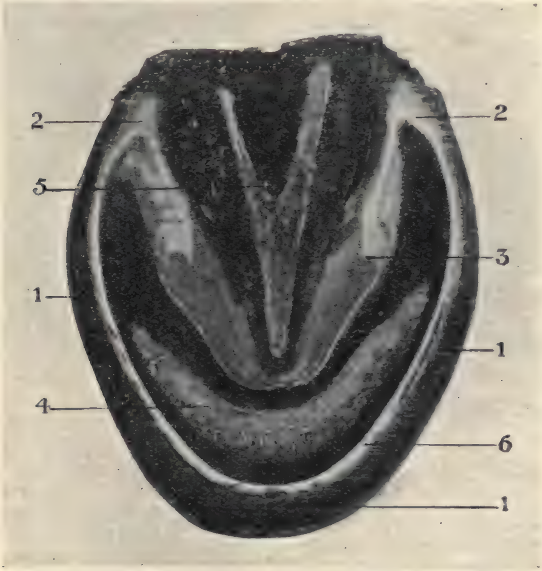


FIG. 231.—HORIZONTAL SECTION THROUGH THE FOOT, ONE INCH ABOVE AND PARALLEL TO THE GROUND.

1, The wall; 2, its inflections at the heels; 3, the bars and convexity of the sole caught in the section; 4, part of the pedal bone; 5, portion of the plantar cushion; 6, the white inner layer of horn between the sensitive laminæ and the outer wall.

The **Foot-pad**, or 'frog,' as it is vulgarly known, is a pyramidal-shaped piece of horn, accurately moulded over the plantar cushion, and filling up the space left by the inflection of the wall at the posterior part of the foot (Fig. 228, *1*, *2*, *3*, *8*). In the foot-pad we meet for the first time a peculiar soft elastic horn, possessing something of the characters and appearance of india-rubber. The horn fibres of this structure are wavy, arranged in strata which run at right angles to each other, and confer on the part its fibrous character and elasticity. The horn of the pad contains much more moisture than that of any other part of the foot, and it is the moisture which confers on it its peculiar soft pliable condition, aided by the secretion of the sweat glands of the plantar cushion. The foot-pad grows from the vascular membrane covering the plantar cushion. The overgrowth of horn is provided against by a method which is a combination of that found in the wall and sole—viz., it is cast off after growing to a certain thickness, while the part next the ground is worn away by friction. In consequence, owing to its rubber-like nature, rags of horn along the edges of the foot-pad are a common and natural condition.

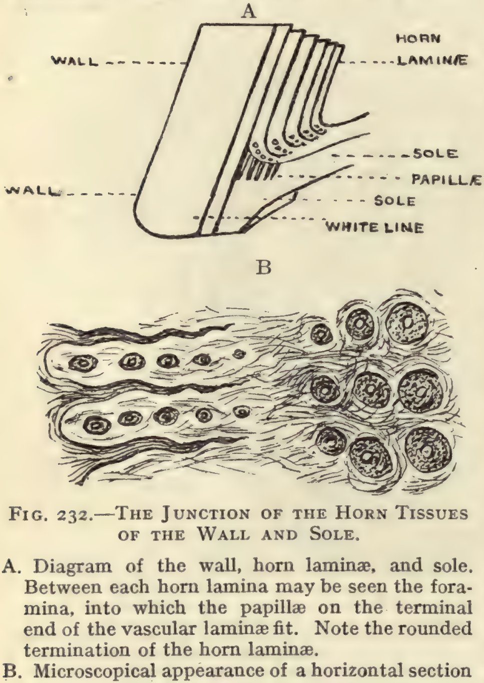


FIG. 232.—THE JUNCTION OF THE HORN TISSUES OF THE WALL AND SOLE.

A. Diagram of the wall, horn laminæ, and sole. Between each horn lamina may be seen the foramina, into which the papillæ on the terminal end of the vascular laminæ fit. Note the rounded termination of the horn laminæ.

B. Microscopical appearance of a horizontal section of the junction of wall and sole; the horn laminæ are wavy, devoid of secondary laminæ, and between each may be seen the papillæ in section. On the right of the figure the horn tubes of the sole are shown.

A transverse section of the foot-pad at its posterior part resembles in appearance the letter **W**. The two lower points are the sides of the pad; the space between them is the so-called 'cleft,' or central depression (see Fig. 233, *3*). Above the cleft on that side of the pad next to the sensitive foot is a projection of horn known as the '**frog-stay**,' or 'peak.' The function which has been assigned to this peak is to prevent the parts becoming displaced; but its position, shape, and connection suggests that it acts the part of a wedge, being forced upwards under pressure when the foot comes to the ground, and it may thus exert a central pressure on the plantar cushion and assist in the expansion of the foot. But it appears, however, to be more valuable as a means of stimulating the nerve-endings in the plantar cushion, which are especially abundant in this region, and so acting the part of a touch organ.

The Structure of Horn.—The horn of the foot consists of epithelial cells which have undergone compression and keratinisation, by which latter process they become hard and tough. It is possible to have horn in the foot which is not keratinised, and the two are very readily distinguished by the process of staining. The double stain picro-carmine has a selective affinity for each kind of horny tissue; the carmine picks out the protoplasmic and non-corneous cells and stains them red, whilst the picric acid stains all tissue a yellow colour which has undergone the process of keratinisation. By means of this stain it is easy to determine the character of the horn under examination.

The ultimate horn cell is a very thin, spindle-shaped, oblong, or irregular body (Fig. 234), containing granular matter, a nucleus, and frequently pigment. In all cases the cells are united at their edges and sides by a cement substance. By acting upon horn with caustic alkalies, the cells are in the first instance rendered clear; they then gradually dissolve, are converted into a gelatinous mass, and finally disappear. Bearing in mind the highly alkaline nature of decomposing urine, owing to the presence of free ammonia, the

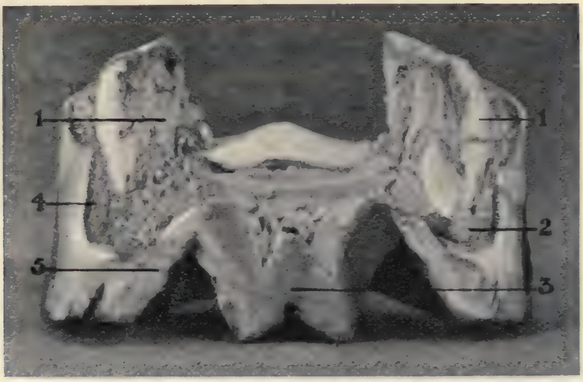


FIG. 233.—VERTICAL SECTION THROUGH THE FOOT, AT A POINT TWO-THIRDS THE DISTANCE FROM THE TOE TO THE BULBS OF THE HEEL.

1, The lateral cartilages; 2, heel of the pedal bone; 3, the foot-pad; 4, the sensitive laminæ; 5, the 'bars.'

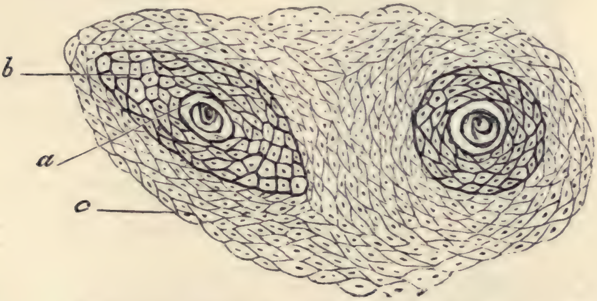
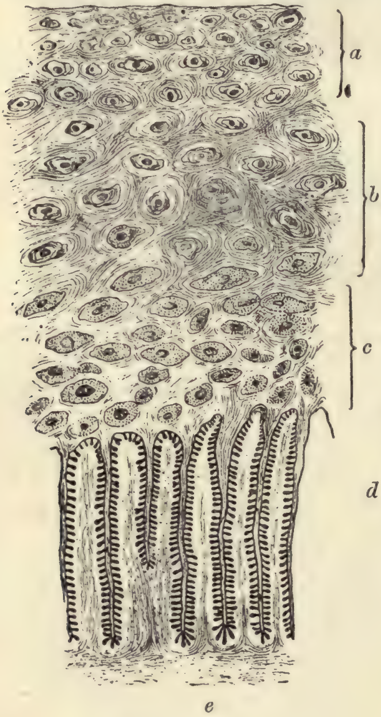


FIG. 234.—HORIZONTAL SECTION OF THE HORN OF THE WALL, HIGHLY MAGNIFIED.

a, Horn tube, a canal containing cellular elements; *b*, the tubular horn—that is, the horn secreted from the papillæ, forming an oval or circular nest of cells around the canal; *c*, the intertubular horn.

practical application of this fact in the care and management of the feet is very obvious.

If a portion of horn be examined microscopically, it is found that the compressed epithelial structure is tunnelled in such a way as to form canals or tubes, or, at any rate, to form a structure which is tube-like in nature (Fig. 235). These tubes exist wherever the growing surface is invested with papillæ, so that where the papillæ are numerous the tubes are numerous, where they are absent the tubes are absent. The only horny structures not secreted from a papillated surface are the horn laminæ, and consequently in these there are no horn tubes; everywhere else the horn is found to possess a more or less tubular structure. The method of tube formation is simple. The papillæ growing from the various secreting surfaces are lodged in canals in the horn. As the horn grows down from the surface which secretes it, the canal enclosing the papilla gradually slides off, but throughout the length of the horn a tubular appearance indicates where the papilla was at one time lodged, and the cells of these tubes, from their reaction with carmine, prove themselves to be different to true horny structure.



a, b, c, The outer, middle, and inner portions of the wall, showing the canal system with the tubular and intertubular horn; *d,* the horn laminæ bearing on their side the lamellæ, shown black: there are sometimes a few short laminæ to be seen — one is shown in the figure; *e,* the sublaminal tissue, from which the sensitive laminæ may be seen dovetailed between the horn laminæ, and from the sides of which the sensitive lamellæ grow.

FIG. 235.—HORIZONTAL SECTION OF THE HORN AND VASCULAR WALL OF THE HORSE'S FOOT. LOW MAGNIFICATION.

The horn which is secreted in the foot is therefore formed (1) from papillæ found on the secreting surface, and (2) from the spaces between the papillæ. The papillæ form tubular horn, the spaces between them form intertubular horn (Fig. 234, *b* and *c*), and this is arranged in an oval or concentric manner around the canal (Figs. 235 and 236), the cells composing it being so placed that their edges are towards the papillæ. There is, however, a layer of cells which actually forms the wall of the canal, and these are arranged with their sides next it; or, to put it another way, they stand on their edges. In the deep layer of the wall the papillæ produce a much greater secretion, and here the circular or oval masses of cells investing the canal are more prominent; and, further, unlike those in the anterior and middle parts of the wall, they need no reagent to demonstrate their cellular nature (Fig. 235, *c*). If a section of wall be stained with picro-carmine, only the canal contents of the external and middle wall stain with carmine; all the remaining substance takes up the picric acid. In the deep wall this is different; here the whole of the cellular material secreted by the papillæ is stained red, showing that these cells are protoplasmic rather than horny, and partly accounting for the fact that this deep horn is always softer than the middle or external horn of the wall.

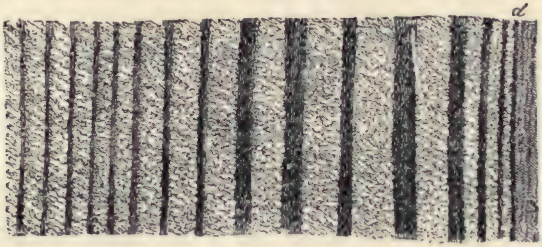


Fig. 236.—Microscopical Structure of Horn: Longitudinal Section of the Wall. Low Magnification (after Lungwitz.)

Note the different size of canals; those on the right are nearest the laminæ; those on the left are towards the outside wall; they are smaller and more numerous than those deeper seated; *d* is a portion of a horn lamina.

If a vertical section of horn be made, the canals are now seen divided in their length (Fig. 236). Though spoken of as canals or tubes, they are really not empty, but throughout their entire length contain cells which are protoplasmic in nature. These, owing to the manner in which they reflect light, give to the part a beaded appearance. The cells contained within the canal are secreted by the apex of the papilla; they do not fill up the entire lumen of the canal. The use of the canal system in horn is for the purpose of irrigation; the horn must be supplied with moisture; the bulk of this is obtained through these imperfect canals, the soft protoplasmic canal-wall readily admitting transudation. It is not intended to assert that anything like a fluid is circulating along the tubes, but moisture certainly does find its way down, and is readily imbibed by, the surrounding cells. Besides this arrangement for maintaining the moisture in horn, there is no doubt that in the intertubular horn moisture passes from the secreting surface from cell to cell, and in this way is transmitted throughout the length of the foot. It can also be absorbed from without. Constant evaporation is taking place from the foot, and its loss is made good in the manner indicated. If the invisible moisture which is always escaping from the foot be hindered in its evaporation, the horn becomes sodden, crumbles away, and resembles a grey cheese-like mass. This experiment can be readily performed on the sole and foot-pad by accurately moulding to their surface a sheet of gutta-percha and leaving it there. The practical lesson is obvious: no impervious material should be applied to the foot as a protection, or, if used, it should be ventilated.

Use of the Moisture in Horn.—The amount of moisture contained in horn is something considerable, and the rate at which it evaporates is remarkable.* If parings of the foot-pad be enclosed in a bottle, in a short time the interior will become bedewed with moisture. The use of the moisture is to maintain the elasticity of the foot, and prevent the part from becoming brittle. The agencies which are at work to prevent the too rapid evaporation of moisture from the wall are the thin, varnish-like layer which covers the hoof, and the natural hardness of the external fibres of the wall. Horn containing but little moisture is in an abnormal condition; it is rigid and brittle; nails driven into the part cause it to crack, and the elasticity, on which the natural shape and usefulness of the foot so largely depends, becomes impaired, or even destroyed. A museum specimen of a foot illustrates these facts very clearly; in its dried condition it is so brittle that, if dropped, it will frequently fracture like a piece of glass; but if this foot be placed in water for a few days, it comes out as fresh and elastic as though it had just been removed from the body. All that the horn has done is to imbibe water, and the previously brittle substance now becomes yielding and elastic. The entire physiology of the horse's foot is centred around this question of the moisture contained in horn. The presence of moisture confers elasticity, and elasticity of the hoof prevents its fracture under the pounding effects of concussion during work.

Chemistry of Horn.—An analysis of the horn of the foot has given us the following results:†

	Wall.	*Sole.*	*Foot-pad.*
Water	24·735	37·065	42·54
Organic matter	74·740	62·600	57·27
Salts	0·525	0·335	0·19
	100·000	100·000	100·00

The pad contains the largest amount of moisture, and the wall the least. The salts are small in amount, and consist principally of those of sodium, magnesium, iron, and silica, in the form of chlorides, sulphates, and phosphates. Keratin, a substance which replaces the protoplasm originally existing in the cells, is a protein-like body found in hair, nails, and even, in a modified form, in the nervous system; it consists of carbon 51·41, hydrogen 6·96, nitrogen 17·46, oxygen 19·49, and sulphur 4·23, per cent. The sulphur is loosely combined, and it is this, in combination with hydrogen, which causes horn undergoing disease to have such an offensive odour, sulphuretted hydrogen being formed. Keratin is a very insoluble substance, but is dissolved by strong and boiling acids and by alkalies. With sulphuric acid it yields leucine, tyrosine, and volatile substances, the latter conferring the peculiar odour on burnt horn, feather, nail, etc.

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* James Clark ('Observations on the Shoeing of Horses') described the moisture in the foot in 1782. He speaks of the insensible perspiration exuding, and states that if a newly-pared piece of frog be held up to the light of the sun, vapour may be seen arising from it.

† 'Chemistry of the Hoof of the Horse,' *Veterinary Journal*, vol. xxv., 1887.

Provisions for Elasticity and Toughness.—From what has previously been said, it can be seen that it is the wall of the foot which supports the horse's weight. On examining the wall, it is found to be thickest at the toe, thinner at the quarters, and thinnest at the heels (Fig. 239); it is thickest at the toe owing to the functions performed by this part, leading to excessive wear and tear. As the pad and posterior part of the foot are the first to make contact with the ground (at any rate, in all fast paces), so the toe is the last part to leave it, the final propulsion being given by it to the body, as we have seen in studying locomotion. The object of the wall becoming thin towards the posterior part of the foot is to allow of the elastic movement which has yet to be described. Two physical conditions have to be provided for in the wall—*i.e.*, elasticity of the posterior part and toughness of the anterior portion. The first is furnished by the wall being thinner at the heels than elsewhere; but besides being thinner, the wall of the heel contains more moisture than the wall of the toe, and this moisture ensures its elasticity. The younger the horn—viz., the nearer to the coronet at which it exists—the more moisture it contains; the farther away from the coronet, the less moisture it possesses, and the tougher and more resisting the horn.

The wall grows evenly from the coronet all the way round; if it grows ½ inch in the month at the toe, it grows the same length at the quarters, and the same at the heels. The anterior part of the wall is longer than the posterior, therefore the anterior is tougher than the posterior, for the reason that the horn is much older at the extremity of the toe than it is at the heel, and being farther away from the coronet, it contains less moisture. The wall at the heel is some months younger than that at the toe; it is thinner and contains more moisture, therefore it is more elastic, but not so tough. The age of the wall is an important factor in the wear of the foot. If it takes from nine to twelve months for it to grow from the coronet to the toe, the piece of wall at *f′*, Fig. 237, is, say, twelve months old, whilst that at *a′* is less than six months old. The horn of the quarter is older than the horn of the heel, and the horn of the toe older than that of the quarter. This provision admits in the unshod foot of considerable friction occurring at the toe without producing undue wear, for the part is hard and tough, while the younger and moister horn at the posterior part of the foot allows of elasticity. In this way the ground surface of the foot is provided with the hardest horn where friction is greatest. In theory, no fraction of an inch of the ground surface of the foot, from toe to heel, is of quite the same age.

The toe of the wall appears to grow faster than either the quarters or the heels, but this is more imaginary than real; it is the tendency of the foot to grow *forward* as well as downward which produces the illusion. That the foot grows forward may readily be determined by experiment, for if a cut be made in the wall at the coronet, say an inch or so from the heels, it will in course of time be carried some considerable distance towards the toe; the exact amount can be determined by observing the obliquity of the horn fibres.

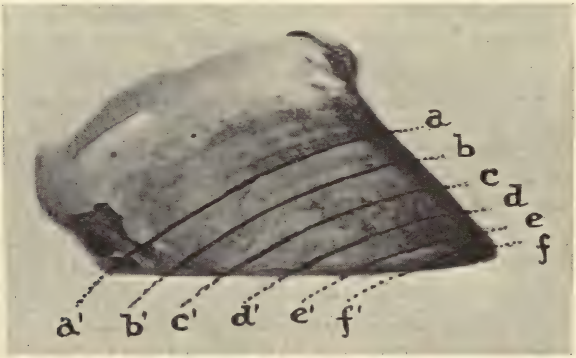

FIG. 237.—DIAGRAM ILLUSTRATING THE AGE OF THE WALL.

a, b, c, d, e, f, are circles drawn round the hoof parallel to the coronet; in this way it is ascertained that the age of the wall at *a* is the same as the heel at *a'*; the age of the wall at *d* corresponds with the age of the quarter at *d'*. Every portion of the ground surface of the wall is of a different age, being oldest and hardest at *f'*, and youngest and most elastic at *a'*.

How the Weight is carried by the Foot.—It is universally recognised that the weight of the body is supported by the union of the insensitive with the sensitive laminæ. That the enormous weight of the horse's body should be carried upon—or, rather, slung upon—thin delicate strips of sensitive material on the one hand, and correspondingly delicate strips of horn on the other, is perhaps the most remarkable feature in the physiology of the foot. This union is so firm that it is a matter of extreme difficulty to separate the two surfaces, even by mechanical means. In a single foot the weight is carried on 600 or more primary laminæ, assisted by 72,000 or more secondary laminæ. Those laminæ situated at the anterior part of the foot are exposed to more strain than those posteriorly placed, for the reason that, during progression, the final propulsion of the body comes entirely on them ; they are also longer, and have no plantar cushion or foot-pad to assist them, as the shorter, posteriorly placed laminæ have. The latter have their strength increased by the direction in which the weight of the body comes upon them. Instead of bearing it on the length of the laminæ, as at the toe, they carry it on the side, in such a manner that the work of one lamina at the toe is shared by several at the quarter.

It will be remembered that the laminæ are mainly attached at the anterior and part of the lateral face of the foot to bone, but on the remaining lateral face and posterior part of the foot they are attached to stout cartilage ; if a line be drawn through the foot at the junction of these structures (Fig. 238), this feature will be demonstrated ; part of the laminal attachment is cartilaginous and part osseous, the cartilaginous portion being situated where elasticity is required—viz., the posterior face of the wall. The line between hair and hoof shown in the figure indicates that part of the lateral cartilage is within and part outside the hoof. One function of the lateral cartilages of the foot is to afford a movable wall-attachment to the sensitive laminæ, and enable them to be carried outwards during expansion. A knowledge of the relation of the posterior laminæ to the

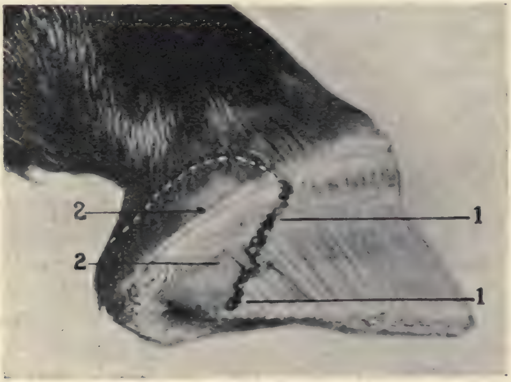

FIG. 238.—THE RIGID AND YIELDING PORTION OF THE FOOT.

1, 1, The line of the lateral cartilage, ascertained by passing pins through the laminæ into the junction of the cartilage with the bone ; 2, 2, the portion of the vascular wall, coronary body, and skin covering the lateral cartilage. The part of the lateral cartilage extending above the hoof has its upper edge outlined, but the dotted line is too straight (see Fig. 219).

lateral cartilage explains the cause of lameness in 'side-bone'—viz., the squeezing of the sensitive structures between the wall on the one hand and the ossifying cartilage on the other.

The folding up of the horny and vascular leaves in the foot, in the manner previously described, has another function besides that of merely supporting the weight and rendering the union firm. Reference has previously been made to the remarkably small size of the horse's foot in proportion to the size of his body. Comparing the horse's foot, so far as size is concerned, with the human foot, the advantage in the majority of cases lies on the side of the biped. The most interesting fact which physiology has to demonstrate is that, though the foot presents a small circumference, in reality it encloses a vast area, due to the anatomical arrangement of the laminæ. It is clear that by the process of folding up material within, the surface of the foot is considerably increased. In other words, by this arrangement the foot has been kept within small proportions without affecting its strength. A book, say of 600 pages, may, by placing one leaf on the other, be made to occupy a bulk represented by a few inches; but if each page be laid out separately on the ground, and made to touch the others, the surface covered will be considerable. This is exactly what occurs in the foot; the insensitive and sensitive leaves by their singular arrangement increase the surface of the foot, and yet keep it within reasonable limits. Bracy Clark, one hundred years ago, was the first to recognise this provision, and had a calculation made as to the increased surface afforded, which was considered to be equal to 1½ square feet. Moeller* has estimated that it is equivalent to 8 square feet, whilst Gader's estimate† is 10¾ square feet. For safety Moeller's number is adopted. The bearing surface afforded by each foot is equivalent to 8 square feet, giving a total area of 32 square feet. It is evident, that as feet vary greatly in size, this surface must accordingly be greater or less.

The physiological function of the leaves of the foot is demonstrated by pathological observation. Inflammation of the laminæ, apart from septic or intestinal poisons, occurs either through severe work or through an animal standing too long in one position; in either case the parts get strained. The practical value of exercising horses which from any cause have to stand for a length of time is well known; exercise overcomes the tendency of the laminæ to congestion from continual strain, and the feet not only become cool, but the animal may continue standing for a considerable time if exercised daily. The treatment of laminitis by exercise possesses a sound physiological basis. If any doubt exists as to the function of the laminæ in supporting the weight of the horse's body, it is only necessary to look at the processes which occur in them as the result of disease. Laminitis is often attended by separation of the laminæ, when, the horse's weight being no longer properly supported, the pedal bone under its influence is actually forced through the sole of the foot.

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* *Op. cit.*

† Goubaux and Barrier, 'Exterior of the Horse' (translation).

The Use of the Bars.—The inflected portion of the wall, known as the 'bars,' runs, as we have previously mentioned, forwards under the foot instead of completing the circle of the wall. The object of this non-completion of the ring the wall originally gave promise of forming, is to allow of expansion of the foot by making room for the elastic posterior foot—viz., the plantar cushion and foot-pad. The explanation why the wall is turned in instead of ending abruptly, is to afford a solid bearing to the posterior part of the foot, to give additional strength, and to secure a more intimate union with the sole. The bars, being part of the wall, are intended to bear weight, and in consequence in the foot of the wild horse and zebra they present the most extraordinary development.

The **Use of the Sole** is quite clear: it is to afford protection to the sensitive parts above. Its normally concave shape (Figs. 229 and 230) proves that it is not intended to bear on the ground over its general surface, and the acute lameness which results from a stone in the foot gives further proof, if any were required, of its indifferent weight-supporting properties; that margin, however, in contact with the wall can bear weight, as there is no sensitive part immediately above it (see Figs. 229, 230). Under the influence of the body weight the sole becomes slightly flatter, especially that portion of it situated posteriorly in the horns of the crescent. When the expansion of the foot is studied, the object of this flattening will be more apparent.

The Use of the Foot-pad.—This is one of the chief anti-concussion mechanisms in the foot; it is there to prevent jar, and it does so by receiving, in conjunction with the posterior wall, the impact of the foot on coming to the ground; this is imparted to the plantar cushion, and through the lateral cartilages to the wall of the foot, which bulges or, as it is termed, expands (see Fig. 239). In breaking the jar (not only to the foot but to the whole limb), it is assisted by its elastic, rubber-like nature. The foot-pad needs for its perfectly healthy condition contact with the ground; it is strange that in this respect two structures situated side by side —viz., the sole and pad—should be so opposed in function. If the foot-pad be kept off the ground, the part atrophies, the heels contract, the foot is rendered smaller, and the pad becomes diseased. This wasted condition of the pad and narrow foot may be restored by pressure, but that pressure must be ground pressure. It is possible by means of a bar-shoe to throw considerable pressure on the pad and heels, but the foot still contracts; it is only when the pad is bearing on the ground that it continues in a healthy condition, and retains its normal size. Foot-pad pressure is, therefore, one of the rules in shoeing if the part is to be able to exercise its natural functions. In thinking of the foot-pad as a buffer, sight must not be lost of the fact that it affords protection to the joints and flexor tendon of the foot, matters of vital importance. The position of these relative to the foot-pad is seen in Fig. 220.

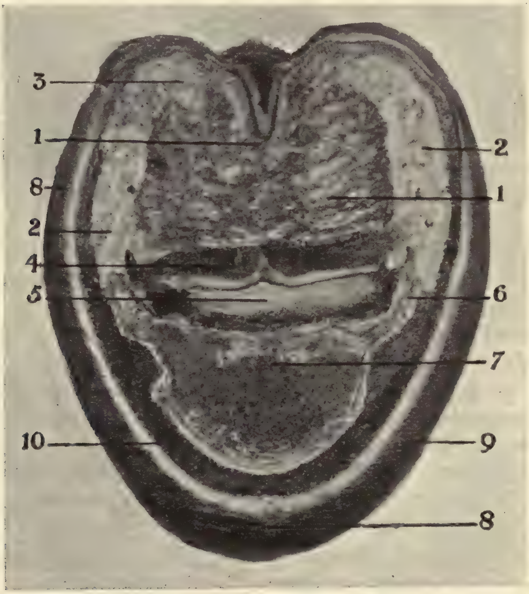

FIG. 239.—HORIZONTAL SECTION THROUGH THE STRUCTURES OF THE FOOT PARALLEL TO THE GROUND AND TWO INCHES ABOVE IT.

The plantar cushion, 1, 1, practically occupies half the foot, and is lodged between 2, 2, the lateral cartilages: these may be seen extending forward and attached to the wing of the pedal bone at 6; they end posteriorly at 3, fusing with the plantar cushion; 4, cut surface of perforans tendon; 5, cut surface of the navicular bone; 7, the pedal bone; 8, the white line, extending around the wall from heel to heel; 9, the wall: note the difference in thickness between the toe and the heel; 10, the vascular laminæ.

Use of the Lateral Cartilages.—Those functions of the lateral cartilages which have already been referred to may be summarised as follows: These structures form an elastic wall to the sensitive foot, and attachment to the vascular laminæ; they also admit of increase in width occurring at the posterior part of the foot without destroying the union of the two sets of leaves. Further, by their connection with the vascular system of the foot, their elastic movements materially assist the circulation. The primary use of the lateral cartilages is to render the internal foot elastic, and admit of its change in shape which occurs under the influence of the weight of the body. The alteration in the shape of the foot is brought about by pressure on the pad, which widens and in consequence presses on the bars. The pressure received by the pad is also transmitted to the plantar cushion, which likewise flattens and spreads under pressure. Both of these factors force the cartilages slightly outwards. When the posterior wall recoils the cartilages are carried back to their original position. Should this elastic cartilage under pathological conditions become converted into bone, its functions are destroyed, and lameness may occur. It can be demonstrated that by surgical interference the hoof can be made permanently wider, and thereby rendered capable of accommodating lateral cartilages which have undergone an increase in size as the result of ossification.*

Anti-Concussion Mechanism.—The special physiology of the foot is a consideration of the factors whereby the parts are saved from concussion, in spite of wear and tear, batter and jar. The weight carried on each fore-foot when the horse is standing is rather more than one quarter the weight of the body; during locomotion the amount varies from half the weight in the trot to the entire weight in certain stages of the canter and gallop. The mechanisms which exist in the foot to save concussion are not only intended for the protection of the foot, but also to save the limb, and they may be tabulated as follows:

1. The yielding articulation in the pedal joint.
2. The increase in the width of the foot when the heels come to the ground, known as expansion.
3. The elastic foot-pad.
4. The slight descent of the pedal bone, and with it the sole.

Expansion is a term warranted by custom, though perhaps not free from objection. It indicates the fact that the foot opposite to the heels becomes wider when the weight comes on them (Fig. 240). The increase in the width of the foot is due to a temporary alteration in the shape of certain of its structures. As a matter of fact, an increase in the width is not the only change which occurs; it can be shown that the heels at the coronary edge sink closer to the ground, while the coronary edge of the wall in line with the toe of the foot retracts, or travels backwards and downwards (Fig. 241, A). In all fast paces, when the foot comes to the ground, the posterior wall and foot-pad first receive the weight. Under the influence of the body weight the foot-pad, as we have seen, is compressed and becomes wider; the plantar cushion with which it is closely in contact is also compressed and becomes wider. The effect of this increase in width is that the foot-pad presses on the bars, while the plantar cushion presses on the cartilages, both of which, yielding laterally, force apart the wall at the heels (Figs. 240 and 241, B). When the weight is taken off the foot the heels return to their original position, and the foot becomes narrower. The increase in width which the foot undergoes is something very small; this is probably the reason why for years its existence has been disputed, especially in this country.* The employment of delicate apparatus such as that used by Lungwitz† and the writer‡ (Fig. 242), and experiments upon feet which have not been mutilated in shoeing, have placed the question beyond all doubt.

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* 'Operation for the Cure of Lameness arising from Side-Bone,' *Veterinary Journal*, vol. xxv. 1887.

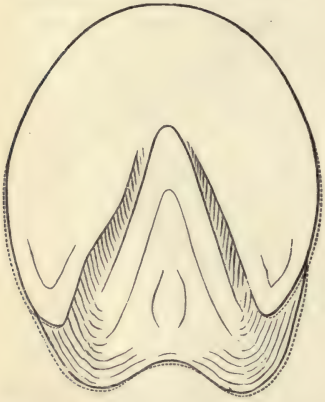

FIG. 240.—DIAGRAM TO ILLUSTRATE THE EXPANSION OF THE FOOT (LUNGWITZ).

The unbroken outline illustrates the shape of the foot at rest; the dotted outline shows the portion of the foot which has yielded laterally under the influence of the body weight.

The area over which the wall expands can be seen in Fig. 241, A; the shaded portion of the heel represents the part which yields laterally. At times expansion can be registered at the coronet, and little or none on the ground surface; but as a rule the amount obtained at the coronet can also be obtained near the ground. As to the amount of expansion no definite statement can be made: it is small and is influenced by the shape of the foot; horses with low heels and full, well-developed foot-pads register a larger amount than where the heels are high and rigid. The measurements obtained by the writer with very delicate

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* Nevertheless, Bracy Clark demonstrated it over one hundred years ago. He says: 'The term "elasticity," however, by its exercise and use will explain, like the principles of gravitation in the hands of the astronomer, nearly everything that before was dark and obscure in the arts of the foot.' W. C. Spooner ('Treatise on the Foot and Leg of the Horse') stated in 1840 that the expansion of the foot was equal to $\frac{1}{12}$ of an inch.

† *The Journal of Comparative Pathology and Therapeutics*, vol. iv., p. 3. 1891.

‡ 'The Apparatus Employed in Inquiring into the Physiology of the Horse's Foot,' *Veterinary Record*, vol. iv., p. 263. 1891.

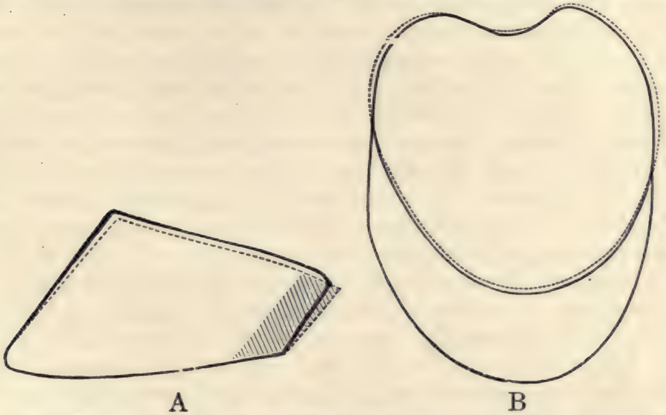

FIG. 241.—DIAGRAMS TO SHOW THE AREA OVER WHICH THE WALL EXPANDS, AND TO ILLUSTRATE THE RETREAT OF THE ANTERIOR CORONARY EDGE OF THE HOOF, AND THE SINKING OF THE HEELS (LUNGWITZ).

A, The unbroken outline shows the shape of the foot with no weight on it; the dotted outline illustrates the retreat of the coronary edge in front and sinking of the heels. The shaded part illustrates the area which expands.

B, In this figure the hoof is looked at from above; the unbroken outline is the coronary edge from heel to heel. The dotted line shows the change in shape it undergoes under the influence of the weight of the body.

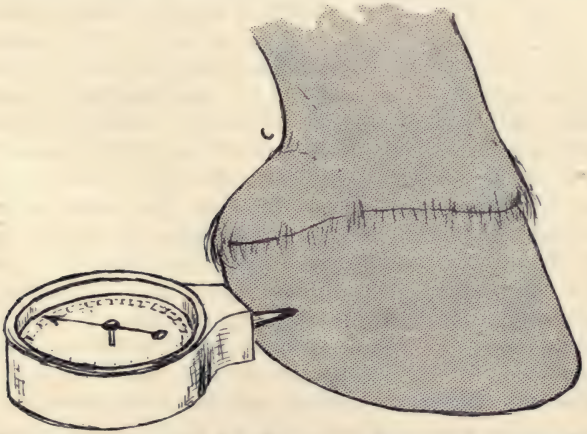

FIG. 242.—APPARATUS FOR MEASURING EXPANSION OF THE FOOT.

The gauge is adjusted to different levels of the wall by means of a block; it registers from $\frac{1}{300}$ to $\frac{1}{25}$ inch.

apparatus were smaller than those obtained in Germany by Lungwitz. On an average there was obtained, by simply lifting up one fore-foot, and so causing the horse to throw double weight on the other limb, an expansion of $\frac{1}{50}$ of an inch for one half of the foot, or $\frac{1}{25}$ of an inch total increase in width. Naturally, during locomotion a greater expansion than this occurs. The question may be asked, What advantage can be gained by such a small increase in the width of the foot? Small as the increase is, it still makes all the difference between a yielding and an unyielding block of horn being brought to the ground; it 'gives' instead of offering resistance, and this 'give' is sufficient to prevent the hoof from being fractured, while the pad which has largely caused the expansion has acted as a buffer and assisted to destroy concussion.

There is no point in the physiology of the foot which has given rise to greater diversity of opinion than the question of 'expansion'; modern investigations completely support the views of the earliest observers. The retraction of the coronary edge of the foot in front and the sinking behind are accompanied by a tense condition of the parts which, since the days of Bracy Clark, have been regarded in the light of an elastic ring or support to the pedal joint. The tense condition is due to the change in the shape of the coronary edge, but whether this is capable of affording support is not evident.

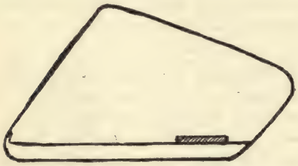

FIG. 243.—EXPERIMENT FOR ASCERTAINING THE COMPRESSION OF THE WALL.

In addition to the changes in the coronary edge of the foot during the period of expansion, another condition is present—*i.e.*, *compression* of the wall under the influence of the body weight, which produces a diminution in its height. This can be roughly demonstrated in the following manner: If a portion of the wall at the heel be cut away so as just to clear the shoe when the latter is fitted, it will be found on placing weight on the limb, by lifting up the opposite fore-foot, that the wall has descended sufficiently to touch the shoe. The experiment may be rendered less free from objection by removing a piece of the wall, as in Fig. 243. If this is made sufficiently large to admit a penny when the foot is off the ground, the coin cannot be introduced into the slot when the weight is placed on the foot. The only explanation which can be afforded is that given above—*i.e.*, the wall has undergone sufficient compression to allow the part which was originally clear of the shoe to come in contact with it, and to produce this it must have diminished in height.

The **Descent of the Pedal Bone** is the last factor employed in saving concussion. The existence of this has been as strenuously denied as the expansion of the wall, but there is, however, no difficulty in demonstrating it; the value of such a function is undoubted. Concussion to the sensitive foot is prevented by a slight up-and-down play between the sublaminal tissue and the pedal bone; as the weight comes on to the foot the pedal bone descends slightly, to rise again when the weight is taken off the limb.* As the pedal bone descends, the sole on which it is resting also descends slightly and comes nearer to the ground; this is one reason why the sole is concave instead of flat. The soft horn uniting the sole and wall specially provides for the slight descent of the sole. The descent of the internal foot saves concussion, in the same way that it is easier to catch a cricket-ball with a retreating movement of the hand than by rigid opposition; further, it facilitates the circulation. The descent of the pedal bone is a most important physiological factor, and one of the safeguards of the sensitive foot.

Vascular Mechanism.—Lying as the foot does farthest from the heart, it is natural to inquire how it is that the blood is able to circulate through it so thoroughly, and whether other means are at hand for assisting the force of the heart in facilitating the circulation. Though the contraction of the left ventricle is sufficient under ordinary circumstances to bring the blood back to the right side of the heart, it is doubtful whether it would be wholly sufficient to empty the foot of blood and keep the considerable plexus of veins full. This plexus is shown in Fig. 226, p. 662, which is a reproduction from a photograph of a corrosion injection.† The figure conveys very accurately an idea of the remarkable venous arrangement of the foot. The venous circulation is assisted by two movements in the foot—viz., the expansion and recoil of the outer foot, and the descent and elevation of the inner foot. There is no difficulty in seeing the movement imparted to a column of fluid circulating in these parts, for if a plantar vein be divided and the horse made to walk, every time the foot comes to the ground the blood spurts out from the vein as if from an artery; when the foot is taken off the ground the stream of blood becomes greatly reduced. A perfect pumping action is in this way produced. The mechanism can also be demonstrated on the dead limb, by placing a manometer tube filled with water in each plantar vein, and then pressing downward on the limb, thus roughly imitating the weight on the leg. With every compression of the foot the water rises in the manometer tubes, and falls during the period of no pressure, a period corresponding in the living animal to the foot being off the ground.

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* Seventy years ago W. C. Spooner wrote: 'On trying the elasticity of the membrane which connects the laminæ to the bone, I found, somewhat to my surprise, that it yielded considerably when pulled downwards and very slightly when pulled upwards' (*op. cit.*).

† The figure appeared in an article by Dr. C. Storch, of Vienna, on 'The Venous System of the Horse's Foot,' *Oesterreichischen Monatschrift für Thierheilkunde*, 1893.

We must accept it, therefore, as a proved fact that the venous circulation is largely facilitated by the expansion and contraction of the posterior part of the foot; during expansion the blood is being driven upwards, and during recoil the veins aspirate the blood into their interior. Indeed, so perfect are these mechanisms that there are no valves in the veins of the foot, and none are found nearer than the middle of the pastern. To assist the circulation, the large venous trunks at the postero-lateral part of the foot are in close connection with the lateral cartilages, and some of the vessels even pass through their substance.

A summary of the physiological features counteracting concussion and facilitating circulation may be stated as follows:

When the weight comes on to the foot, it is received by a yielding foot-articulation, an elastic wall, an india-rubber-like pad, and through these by the plantar cushion. The elastic posterior wall is pressed outwards by the compressed pad and plantar cushion, and it expands slightly from the ground surface to the coronet. At the moment of expansion the bulbs of the heel of the foot at the coronary edge sink under the body weight and come nearer the ground, and as a result of this the anterior coronary edge retracts. The pedal bone descends slightly through its connection with the sensitive laminæ, and presses the sole down with it, while the wall of the foot slightly diminishes in height owing to the compression to which it is exposed. Under these conditions the blood-pressure in the veins of the foot rises, and the vessels are emptied. When the weight is removed from the foot the bloodvessels fill, the pad and posterior walls recoil, the bulbs of the heel rise, and the foot becomes narrower from side to side; at the same time the anterior edge of the coronet goes forward, and the pedal bone and sole ascend.

The **Nervous Supply** of the foot has been mainly worked out by Mettam.* Tactile sensibility has long been known to exist, but the nature of the end organs concerned was unknown. He has shown that these partake of the character of Pacinian corpuscles, arranged sometimes singly, sometimes in groups, and with other positional modifications, which has enabled four distinct methods of distribution in the plantar cushion to be recognised. Pacinian corpuscles have also been recognised in the vascular laminæ and in the skin of the coronet and heel.

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* *Op. cit.*

Valuable as this nerve-supply is in keeping the animal informed of the nature of the ground travelled over, yet it is not essential to progress or safety. All sensory impulses may be cut off from the feet without interfering with the safety of the animal. The inner foot is acutely sensitive to touch, especially the vascular tunics. The plantar cushion is nothing like so sensitive, although Mettam has shown that it is liberally supplied with touch organs.

Physiological Shoeing.—It is impossible to conclude this chapter on the foot without some mention of what may be termed 'physiological shoeing.' By bearing in mind the functions of the various parts of the foot, it is possible to reduce the evils connected with shoeing to comparatively narrow limits. The following rules form the basis of physiological shoeing :

1. The reduction of the wall to its proper proportions, such as would have occurred through friction had no shoe been worn.
2. Fitting the shoe accurately to the outline of the foot, and not rasping away the exterior of the crust to fit the shoe, since this not only renders the horn brittle, but is so much loss of bearing surface.
3. The exterior of the wall should be left intact. The practice of rasping the wall for the *sake of appearance* destroys the horn, and allows of such considerable evaporation from the surface of the foot that the part becomes brittle.
4. The sole should not be touched with the knife ; it cannot be too thick, as it is there for the purpose of protection.
5. The bars should not be cut away ; they are part of the wall, and intended to carry weight. The shoe should rest on them.
6. The foot-pad should not be cut, but left to attain its full growth. No foot-pad can perform its functions *unless on a level with* the ground surface of the shoe.
7. The pattern of shoe is immaterial so long as it has a true and level bearing, and rests on both the wall and bars. The simpler the pattern of shoe, the better.
8. The shoe should be secured with as few nails as its size admits. No more nails should be used than are absolutely necessary, as nails destroy the horn ; further, they should not be driven higher than needful, for high nailing is ruinous to feet.

Such, briefly, are the conditions which fulfil physiological shoeing. The vicious and senseless practice of cutting away the horn of the foot-pad and sole, and thinning the wall by rasping it, are the abuses of shoeing, and are capable of control. The real physiological evil in shoeing, and one which cannot be remedied, is driving nails into the foot.

Pathological.

The diseases affecting the foot of the horse are numerous, and as a rule serious ; they may be connected with the vascular supply, with the bony foundation, with the cartilages and structures around the coronet, with the joint, or with the external cover. Fracture may occur from violence ; injuries arise from shoeing or foreign bodies, and from self-inflicted accidents. **Laminitis** and **Navicular Disease** have been previously touched upon in their physiological bearing. **Ossified Cartilages** have been referred to in connection with the lateral cartilages. **Fistula of the Coronet** is serious, owing to its proximity to the pedal joint, and affecting non-vascular structures like the lateral cartilage; the process is destructive and repair slow. **Suppuration** around the coronet is a formidable affair; the parts allow of very little swelling, are rigid and unyielding, and burrowing of pus occurs such as is hardly met with elsewhere. It is the dread in all foot injuries, and is brought about by the manner in which the parts are confined within an unyielding box. There are few diseases more painful, and few of which the surgeon has more genuine dread. Suppuration may follow any injury, from an injury in shoeing to a tread on the coronet. **Injuries in Shoeing** are generally caused by the nail, occasionally by the foot being over-reduced. A shoeing injury causes intense pain, and, if severe, is followed by considerable destruction within the foot. A frequent injury in the angle between the bar and wall is caused by the heel of the shoe, and known as **Corn**; it is due to sole pressure, which in this region especially cannot be tolerated. It is a bruise of the part which is very persistent, and frequently permanent. It has a physiological basis; the foot grows forward (p. 674); it carries the shoe forward, and so takes it off the bars. The heel of the shoe then beds itself into the angle formed by the sole between the wall and bar. **Bruise of the Sole** may occur at any other part of the sole, but is never followed by permanent results, as is a corn. The sole cannot withstand pressure, especially that caused by a stone becoming wedged between the foot-pad and the shoe. **Arthritis** from penetrating wounds of the foot is common, but the pedal joint does not suffer from locomotive arthritis, as does, for instance, the joint immediately above it, and many others in the body. Nor do the foot-joint or tendons suffer from sprains, though, under the influence of erosion after neurectomy, the tendon of navicular disease may be worn through and snap, or even the bone fracture. **Fracture of the Pedis,** in spite of its porous nature, is very rare. When it does occur, it rarely unites, though the parts are contained in a permanent splint, which, theoretically, should lead to perfect union. The fact, however, is that, under the influence of the body weight, the fragments are always being forced apart. Nutritive changes occur in the foot after neurectomy, and the hoof may come off; or so-called **gelatinous degeneration** of the foot and limb occur as high as where the nerves are divided. **Evulsion** of the healthy foot may occur as the result of an accident, the foot being caught, for instance, in railway-points, and the animal, in its struggles, pulls the inside foot out of its cover. In such cases the nails in the wall afford such a powerful hold that, rather than allow the shoe to tear away, the hoof is pulled off—an object-lesson in the security afforded by nails, and the hopelessness of ever attaching the shoe by any other means so simple and effective.

A weak wall in the fore-foot is liable to fracture during dry and hot weather; it is known as **Sand-crack,** and its physiology will be understood when the necessity for moisture in the horn is borne in mind (p. 671). The crack always begins at the coronet; it opens and closes in accordance with the expansion and recoil of the foot, and demonstrates these movements. Sand-crack in a hind-foot is a totally different matter; it occurs at the toe, extends from bottom to top, and is due to violence, especially in heavy draught. **Contraction** of the foot was the great bugbear in days gone by. It was regarded as a disease; in the present day it is almost entirely a symptom. A foot will contract if it is rested, as in navicular disease, and the cause of this must be evident from what has been said in the previous pages. If the foot-pad be cut away in shoeing and no pressure given it, contraction occurs as a result, in consequence of loss of function of the food-pad and plantar cushion. Inflammation of the glands of the plantar cushion leads to an offensive discharge known as **Thrush,** which erodes what is left of the horn of the foot-pad. This condition is aggravated by dirt, and is therefore common in the hind-feet, but its chief cause is a want of proper foot-pad pressure. The horn of the sole and foot-pad, from causes which are not clearly known, but probably microbic, takes on an unhealthy, cheese-like, and offensive condition, due to disease of the horn-secreting membrane of these parts. It is a most intractable disease, known as **Canker,** and is frequently associated with defective hygienic care. The layer of white horn at the toe between the insensitive laminæ and the outside wall is liable to a curious disintegration known as **Seedy Toe,** which, by extension, may excavate the wall nearly as high as the coronet. It is a slow process, and recovery is tedious. The hoof frequently shares in any general disturbance of the system. There is a tropical form of skin disease in which the hoofs frequently indicate by the scaly condition of the wall that the horn-secreting substance—a modified skin—is sharing in the general disorder. Similarly, the growth of the feet may from constitutional causes be temporarily inhibited, and then start again with renewed vigour ; every increase in the production of the wall being marked by a ring which extends all round the hoof. From the same cause, horses exposed to standing in wet places like marshes have an impetus given to the growth of the wall, resulting in rings on the feet.

The above indicates the numerous diseases or injuries to which the foot is liable. The foot has a special pathology, as well as a special physiology. It is the most common seat of incurable lameness, and has always been so since the horse was domesticated. 'No foot, no horse,' is as old as the days of Xenophon. This horse-master tells us how to keep the horn of the feet of cavalry horses hard—a very necessary matter at a time when shoes were unknown. It is a remarkable fact that the horn of unshod feet is infinitely harder than that of horses wearing shoes. It may, indeed, be so hard as to resist the entry of a nail.

CHAPTER XVIII

GENERATION AND DEVELOPMENT

THE **Sexual Season** of female animals is a subject which in recent years has received exact expression at the hands of Heape,* whose communication, quoted below, we have followed in connection with this question. Heape divides female mammals into two classes—*Monœstrous*, or those which have one œstrous cycle, and *Polyœstrous*, or those having a series of œstrous cycles. The first phase of generative activity at the beginning of a sexual season is known as *Proœstrum*, or the *proœstrous period ;* it corresponds to the period 'coming on heat,' or 'coming in season.' The period lasts a variable time in different animals, and is succeeded by the *period of desire*, or *Œstrus*. It is only during this period that sexual intercourse is permitted, or that fruitful coition is possible. If conception does not occur or is prevented, œstrus is followed by *Metœstrum*, or the *metœstrous period*, during which sexual activity passes away, and is succeeded by a period of complete rest or freedom from sexual excitement, known as *Anœstrum*. The anœstrous period may last two, three, eleven, or more months, depending on the species.

The sexual cycle is not always as above described ; there are animals in which metœstrum is not followed by a period of complete rest, but by a short quiescence, known as *Diœstrum*, which lasts a certain number of days, and is then followed by a new proœstrum, œstrus, metœstrum, and diœstrum. Among monœstrous mammals is the wolf, which in the wild state has only one sexual season in the year. Another is the dog, though in this case the sexual season may recur during the year ; but the periods in each case are quite distinct, and followed by complete rest, which is the essentially distinguishing feature. Among polyœstrous mammals are the mare, cow, sheep, pig, and all of these during a portion of the year exhibit a series of diœstrous cycles (in the absence of pregnancy), followed by anœstrum until the next year. The number of annual sexual cycles which any given species passes through is vastly influenced by domestication. Probably in all primitive species one sexual season yearly was the rule. Domestication alters this. The abundant food supply renders the struggle for existence no longer acute, the dread of being preyed upon by the enemies peculiar to each species is removed, and one of the responses to these altered conditions is a greater desire to multiply, for the reason that the energies previously expended in the struggle for life are turned into a fresh channel. The cat in a wild state has one sexual period a year; the domestic variety has three or four. The wild dog and wolf breed once annually, in captivity twice annually. The lioness in a wild state has probably but a single breeding season; in captivity the œstrous period may be three or four times a year. Bears in a wild state have a single breeding season, in captivity more than one. The wild otter has a single season, but in a state of captivity she comes 'in season' every month (Marshall and Jolly). So far, in fact, as evidence is available, a single sexual season for animals in a state of freedom appears to be the natural condition, *polyœstrum* being an acquired character. The frequency of œstrus under domestication is essentially influenced by food, temperature, and environment.

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* 'The Sexual Season of Mammals,' etc., by W. Heape, M.A., *Quarterly Journal of Microscopical Science*, vol. xliv., p. 1, 1901.

The complete œstrous cycle in the **dog*** under domestication is six months. Every six months, in spring and autumn, the majority of dogs come 'on heat,' though there are many exceptions to this rule, some of the smaller breeds of dogs having a three and four heat period in the year. The period of proœstrum lasts from seven to ten days, and œstrus lasts another week.

In the **mare** the complete œstrous cycle, with its diœstrous intervals, may last for months, in the majority of mares from February to June or July; and unless rendered pregnant, the diœstrous periods last twenty-one days, and are followed by proœstrum, œstrus, etc., as previously described, though the time-duration of these is irregular, generally brief, and always uncertain. For instance, the exact period at which the mare is ripe to receive the male may only be a matter of a few hours, whereas she may be several days in a highly unsettled sexual condition. The mare is in a condition of œstrus on the seventh to tenth day after foaling; with thoroughbred mares it may be the sixth. At this period, though still nursing, she desires intercourse, and in this respect differs from the nursing cow and sow. If she does not conceive, the period of diœstrum is twenty-one days, and is followed by œstrus, the returning heat usually lasting longer by two or three days than the original 'heat.'

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* 'Contribution to the Physiology of Mammalian Reproduction.' Part I.: 'The Œstrous Cycle in the Dog.' By F. H. A. Marshall and W. A. Jolly, *Phil. Trans.*, B., vol. cxcviii., 1905.

The **cow** under domestication will breed at any time of the year (Goodall). She ordinarily takes the bull six weeks or two months after calving, but it is unusual for her to accept the bull while suckling her calf. If the latter be removed or weaned, she shows signs of œstrus six or seven days later, the duration of which may be twelve hours. The period of diœstrum is twenty-one days, at the end of which time both cows and heifers exhibit œstrus. This cycle continues until they are settled in calf.

With **sheep*** œstrus may only last one or two days, or it may pass away very quickly, the diœstrum which follows lasting from thirteen to eighteen days. The number of recurrent periods in any one cycle in the sheep have been observed to depend upon breed ; two, three, or four recurrent periods have been noted. There are some breeds of sheep which may produce two sets of lambs in one year. The period of œstrus may be induced almost at any time in the late summer and autumn by the introduction of the ram to the ewes (Goodall).

The **sow** takes the boar about a week after she has weaned her litter, or about eight weeks after farrowing. The period of œstrus lasts about two days, the diœstrous period twenty-one days.

The only known animal which in a wild state exhibits a continuous series of diœstrous cycles is the monkey, but even in this case the season is limited when conception is possible (Heape).

Cause of Œstrus.—The œstrus period may appear in the dog after a portion of the spinal cord has been excised, proving that it is a process quite independent of any reflex act, that it may exist in the absence of any knowledge on the part of the animal, and that its production is under no central control. Furthermore, such an animal may become pregnant and be delivered in the ordinary way, though quite unconscious of the process. Œstrus and menstruation are produced as the result of an internal secretion derived from the *stroma* of the ovary (see *Corpus Luteum*, p. 698).

The **External Signs of Proœstrum** in all animals are a swelling of the vulva, more or less pronounced, with a slight flow of mucus, which may be blood-stained. There is excitement, The mare may refuse to work, squeals and kicks when approached, elevates and protrudes the clitoris, and micturates frequently, the material being very mucoid. The cow bellows, is excited, and mounts its fellows. Sheep become restless and follow the ram. The dog is playful, excited, and desires the attention and companionship of the males of her own species. In all animals it is only during the actual period of œstrus or desire that copulation is permitted, and in all polyœstrous domestic animals this period is variable in extent.

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* 'The Œstrous Cycle and Function of the Corpus Luteum in the Sheep,' by F. H. A. Marshall, B.A., *Phil. Trans.*, B., vol. cxcvi., 1903.

Changes in the Uterus during Sexual Excitement.—During proœstrum there is an increase in the uterine stroma, injection of the mucous membrane in consequence of a dilatation of the capillaries, and usually a breaking down of the walls of the latter, leading to extravasation of blood into the stroma, or even into the cavity of the uterus. The glands of the uterus swell and pour out a slight secretion. In some animals, such as the monkey, the epithelial lining of the uterus is destroyed during this period; but with ungulates desquamation of the uterus is probably very rare, while in carnivores it occurs more or less in every case. The pigmentation found in the mucous membrane of the uterus after œstrus is due to the extravasation of blood; this blood is also the source of the blood-stained discharge, and on a more extensive scale is the cause of the menstrual flow in monkeys and women, in both of which there is in addition blood collected in lacunæ in the wall of the uterus and destruction of the epithelium. Gradually in all animals the uterus recovers its normal appearance, proœstrum passes away, and is followed by œstrus. Bearing in mind the rapidity with which œstrus may follow proœstrum in such animals as the mare, cow, and sheep, it is evident that the whole of the above process cannot always be fully gone through; but in the dog, whose cycle is far more regular, the uterus undergoes the changes described.

By systematically preventing animals from breeding, the sexual season may be interfered with to the extent of complete cessation (Heape). Certainly the mare used late in life for breeding purposes often proves barren. Yet there are mares which, though deprived of the services of the male, never lose their desire, and may for the greater part of their life be a source of danger from sexual excitement.

Rutting.—When male animals suffer from a periodic sexual excitement, it is known as rutting. This term should be confined entirely to a male sexual season, such as is experienced by the camel, stag, elephant, and ostrich. In the rutting stag the neck becomes enormously swollen (Leeney), the elephant and camel experience a discharge from the temporal gland, and the ostrich becomes red in the legs. All these are at this time dangerous to approach, and frequently violent and aggressive.

Marshall has shown* that a male generative cycle is present in many animals, though not obvious in those under domestication. During the period of 'rut' mature spermatozoa are produced, and probably at no other time. In insectivora and rodents there is a growth of the generative organs, especially the testes, which, if intra-abdominal, may shift position, and appear externally. In the hedgehog appendages like the seminal vesicles assume remarkable proportions in their capacity as secretory organs, shrinking to normal when the period of excitement has passed away.

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* 'The Male Generative Cycle,' F. H. A. Marshall, M.D., *Journal of Physiology*, vol. xliii., 1911.

Cause of Rutting.—There would appear to be little doubt that 'rutting' is due to an internal secretion of the testicle, in all probability elaborated by the interstitial rather than the spermatogenetic cells.

Effect of Removal of Testicles and Ovaries.—The influence of the removal of the ovaries and testicles on general metabolism is a subject which has been referred to in dealing with internal secretions (p. 293), and attention has there been drawn to the fact that both in cats and dogs the complete removal of the ovaries, and, it may be added, of both horns of the uterus, may not in every case prevent an animal exhibiting œstrus. Such, of course, are exceptional cases, for ovariotomy usually suppresses the function. If an animal, for instance, be operated upon before puberty—viz., before an œstrual period has had time to appear—such a one will not subsequently experience any sexual excitement. If the operation be performed during the first pregnancy, the 'heat' period does not occur. If operated upon after one or more œstrual periods, and not being at the time pregnant, there may be a few returning 'heat' periods and free sexual intercourse. If castration of the stag be practised, the antlers fall off from the seventh to the ninth day after operation; fourteen days is said to be the longest time they remain. This is evidence of an internal secretion of the testicle (p. 293), which influences the growth and shedding of the antlers, while the chain of evidence is completed by the fact that castration on one side only affects the growth of the antler on that side. If the epididymis be left after complete castration, its presence modifies the growth of the next pair of antlers.* Similarly, the growth of parts in other male animals is affected by castration. Cats operated upon while very young have heads which are indistinguishable from the female; the tissues of the jowl, which give the head of the male cat such a massive appearance, are lost after castration, and this may occur even when the operation is performed late in life. Female cats operated upon while young acquire a head of the male type, and even if the operation be performed when approaching middle life, there is a disposition to broadening of the skull (Leeney).

The alteration in the shape of the male and female skull observed in the cat when castration or ovariotomy is practised in early life, supports the view advocated by Heape that no being is wholly male or wholly female, but a portion of each sex, with one predominant. Cocks converted into capons when young do not develop such full male plumage, and the combs and wattles are more like those of the hen. Pullets from which the 'clutch' has been taken grow fat, and sometimes put on male plumage. Hen pheasants injured by shot in the ovary have frequently been found with male plumage, and disease of the ovary in hens or pheasants may lead to their crowing (Leeney).

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* I am indebted to Mr. H. Leeney, M.R.C.V.S., for these facts and much other information on the subject.

The **Spermatic Fluid** is alkaline or neutral in reaction, of viscid consistence, contains proteins, nuclein, lecithin, cholesterin, fat, leucine, tyrosine, kreatine, inosite, sulphur, alkaline earths, chloride of sodium, and phosphates. The essential element is the *spermatozoa*, without which the fluid is not fertile. Spermatozoa exhibit spontaneous movement, the long tail moving from side to side, by which means the organism is propelled when placed in the body of the female. The vitality of spermatozoa under suitable conditions is considerable, and when placed in the body of the female they have been found very active many days after copulation. In the bat they remain alive for months, and then impregnate an ovum. Colin found them active in the vesiculæ seminales eight days after castration. The spermatozoa are readily killed by ordinary or acidulated water, glycerin, etc.

The spermatozoa are produced in enormous numbers ; it is estimated in man that each cubic centimetre of seminal fluid contains from sixty to seventy millions of cells. A mature spermatozoon under favourable conditions is active, moving about rapidly in the seminal fluid by means of its long vibratile tail. It is formed of a head, a middle piece or body, and a tail. The head contains the nucleus ; the middle piece the all-important bright spot, the *centrosome ;* the tail is developed to a varying degree in different animals. In the horse the length of the head, which is bluntly pear-shaped, is about 5 μ ;* the tail is eight or nine times as long as the head. The nucleus in the head of the spermatozoon is spoken of as the male pronucleus. The testicular products of hybrids, such as the mule, are infertile, not on account of the absence of spermatozoa, but owing to a defect in the contents of the nucleus (see p. 702).

Seminal Vesicles and Prostate.—It is not known in what way the secretions of the *prostate* and *seminal vesicles* influence the main secretions with which they are ejected, but it is supposed they maintain or initiate the motility of the spermatozoa. The vesiculæ seminales are generally regarded as receptacles for the seminal fluid, but there are animals, such as dogs, cats, and rabbits, devoid of these reservoirs. In the hedgehog Marshall† found that during sexual activity these glands enlarged enormously, and produced a secretion devoid of spermatozoa. He accordingly considers that in this, and probably other animals, the vesiculæ are secretory glands, contributing to the formation rather than the storage of semen. The prostate of the hedgehog was also found during sexual activity to take on cell and tubule proliferation. This periodic development of the accessory generative organs in the hedgehog is regarded by Marshall as due to an internal secretion of the testicle. The prostatic fluid precedes the spermatic in ejaculation, and in stallions and bulls, when excessive daily demands are made, the fluid ejaculated is largely prostatic and infertile.

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* μ=a micron ; $\frac{1}{1000}$ millimetre=$\frac{1}{25000}$ inch (nearly).

† *Op. cit.*

The **Period of Puberty,** or that time in the animal's life when it is capable of procreation, has been put at one and a half years for the horse, eight to twelve months for bovines, and six to eight months for the sheep, pig, and dog. There is, however, a great difference between capability and *fitness* for procreation. Breeding from immature animals is one explanation of a great deal of the worthless material in the shape of horses which may be seen in all countries. The horse is commonly believed to be mature at five years of age; he ought not to be regarded as mature until he has attained his sixth year. Bracy Clark even thought about the eighth year. The ass, according to Crisp, is mature at five years; the ox, sheep, and goat at four; the pig at three. The elephant is generally considered mature at fifty, but Crisp says he does not cut his last tooth until eighty years of age.

The advent of maturity is marked by certain changes in form, particularly in horses. They lose their awkwardness, the outline of the frame becomes more consolidated and in greater unison. In the male the neck becomes thick and curved, the voice deepens, and the whole appearance denotes life and vigour. In both the stallion and bull the temper is usually irritable and uncertain, and often extremely vicious. The age at which procreation ceases is not known. Mares have produced foals at twenty-eight, thirty-two, and thirty-eight years of age,* and it is certain that some good stallions have been advanced in years.

The **Act of Erection** is a vascular phenomenon produced by an engorgement of the erectile tissue of the penis with blood. This engorgement is brought about by stimulation of the *nervi erigentes*, which are derived from the autonomic system, and arise from the sacral portion of the cord. These nerves furnish dilator fibres to the vessels of the penis, and under their influence the cavernous spaces of the erectile tissue become gorged with blood under pressure. The *nervi erigentes* act reflexly through an erection centre in the cord, while the erection centre is under the influence of higher centres in the brain. Erection and ejaculation in the dog may be produced by stimulation of a definite area of the cortex of the cerebrum, and they may also be produced after section of the spinal cord in the lumbar region. The sensory nerves in the penis, by which erotic sensations are carried, are the pudic ; if the pudic nerve be cut, erection, is impossible ; if the central cut end be stimulated, it leads to ejaculation.

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* In a paper on 'The Growth and Maturity of Animals,' by Dr. E. Crisp, referred to above, the writer states he knew a Suffolk cart-mare that bred a foal at the age of thirty-nine (*Veterinary Review and Stockowners' Journal*, March, 1865).

The 'Tartar Mare' was considered to be thirty-four to thirty-six years of age when she bred 'Queen Mab.' 'Driver,' an Australian imported mare, bred 'Moss Rose' at thirty-three (*Standard*, December 25, 1893).

The first portion of the penis which receives the excess of blood in erection is the *corpus cavernosum ;* the spongiosum and glans are not fully erect in the stallion until the penis is introduced into the vagina. The *erector penis* muscle compresses the penis against the pelvis, and by blocking the return of blood assists in maintaining erection (Sisson). At the moment of ejaculation in this animal the glans swells enormously, apparently to cover or grasp the os uteri. After intercourse the organ is withdrawn into its sheath by the contraction of a pair of unstriated muscles, known as the *retractor penis.** Though the organ in the horse assumes such considerable proportions, in the bull this is not marked. The peculiar penis in this animal comes to a narrow point without any of the swelling observable in the stallion. In the act of erection, the **S**-shaped curve of the penis is removed, and the organ elongates ; at the same time the retractor muscles of the sheath draw back the prepuce and the organ is exposed. In the ram, also, the penis is narrow and pointed, and the vermiform appendix at its extremity appears essential for successful impregnation, for if it be removed it is said the animal proves sterile. In the boar the penis terminates in a peculiar corkscrew-like ending. In the dog the increase in the size of the penis is mainly at its posterior part, and the bulbous swelling there observable † is the portion grasped by the spasm of the sphincter cunni of the female, rendering withdrawal impossible until complete relaxation occurs. The bone in the penis of the dog facilitates its introduction into the vagina.

Sexual Intercourse.—Copulation is not necessary in all animals, nor indeed in any. What is required is merely an interchange of elements from the nucleus of two different cells. To this last statement a slight exception might be taken, because there is a condition, *parthenogenesis*, where the access of a second element is not required, but this method of development is unknown in the higher animals. The act of intercourse is of short duration in the majority of animals, excepting the dog, pig, and camel. Colin places it at ten to twelve seconds for a vigorous stallion. It is exceedingly rapid, almost instantaneous, in the bull and ram, probably from the peculiar shape of their intromittent organ. The spermatic fluid is forced into the vagina, or even directly into the uterus. The peculiar termination of the urethra of the horse, and the bulbous enlargement of the glans during the final act of coition, point to the organ grasping the *os* at the moment of ejaculation, while the projecting portion of the urethra is inserted into it, by which means some of the fluid is undoubtedly directly injected into the uterus ; the pointed penis of the bull and ram makes it certain that such is also the case in these animals. An examination of the uterus of the sheep and dog a few minutes after coition has revealed the presence within it of spermatozoa. There is ample evidence that the spermatozoa may remain alive for several days within the uterus. At the moment of intercourse the uterus becomes erect, and the introduction of the male element into it is further assisted by the aspiration following its subsidence. The actual mechanism of ejaculation is produced by a contraction of the vesiculæ seminales, the prostate gland, and probably of the vasa deferentia, through the reflex action of the ejaculation centre in the lumbar and sacral portions of the cord. By this means the seminal fluid is forced out of the vesiculæ into the urethra, and by means of the muscles of the perinæum is forcibly ejected from the urethra. In animals possessing no vesiculæ, such as the dog, ejaculation takes place direct from the testicle and vas deferens.

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* The *retractor penis* muscle is found in the horse, ox, dog, and cat. It has a double source of innervation : motor from the lumbar sympathetic, and inhibitory from the *nervi erigentes*.

† The bulbous swelling is actually the termination of the glans, which in the dog is of considerable length, and extends over the entire length of the *os penis* (Sisson).

The Ovum.—The main function of the ovary is to contain the ova and favour their development. It does not secrete them, the ova are laid down with the other cells of the body very early in the life of the embryo, a portion of material being set aside for their special development, as apart from the cells required for the construction of the other portions of the body. It is a very remarkable fact that within a few hours of the impregnation of the ovum, one of the first acts in the cellular scheme is to provide for the reproduction of the future animal, the prospective parent of which at this stage is a mere mulberry-like mass of cells. The germinal cells, as these are called, as distinct from the body or somatic cells, subsequently form an epithelial layer, which grows into the body of the future ovary as a long cylinder of cells ; these are eventually cut off, and remain in the ovarian structure. At birth the ovaries contain some thousands of eggs, some of which in due course, as the period of puberty arrives, take on further and more active changes. At this time the most advanced cells are enclosed in a follicle containing fluid, the *Graafian follicle.* Lining the follicle is a layer of cells known as the *membrana granulosa ;* at one part these are heaped up, known as the *discus proligerus*, and within this mass the ovum lies buried. The Graafian follicle makes its way to the surface of the ovary, being enveloped in a two-layered cover formed from the stroma of the organ, known as the *theca folliculi*. The cells of the inner layer develop the yellow pigment, *lutein*, which subsequently, on the discharge of the ovum, secrete a yellowish pigment, which stains the cells and fills up the gap left by the discharged ovum.

The mature ovum is very small ($\frac{1}{150}$ to $\frac{1}{120}$ of an inch), yet large enough to be seen by the naked eye. It is therefore one of the largest cells in the mammalian body, though infinitely smaller than the eggs of birds and reptiles. There is a mammal, the 'duck-billed platypus' (*Ornithorhynchus*), which produces eggs the size of a hazel-nut, and the ancestors of all mammals had eggs probably as large. The greater size of the eggs of reptiles and birds is due to the quantity of *yolk*, or *deutoplasm*, they contain, which in mammals is very small in amount, as the embryo of the latter is only dependent upon the yolk-sac for nourishment for a very brief period.

The ovum is a typical cell ; it is spherical, more or less translucent, and contained within a membrane, the *zona pellucida*. The contents, or protoplasm, of the cell consist of fatty and albuminous granules, known as *yolk spherules*, and lying in the protoplasm is a nucleus, containing one or more nucleoli. The nucleus is spoken of as the *germinal vesicle*, the nucleolus as the *germinal spot*. One more body is found in the protoplasm, an *attraction sphere*, or *centrosome*. This latter is extremely small, but its functions are of the utmost importance.

When the rupture of the Graafian follicle occurs, the ovum is flushed out, and at the same moment, according to Henson, the fimbriated extremity of the Fallopian tube becoming erect, grasps the ovary, and thus the escaping ovum is received into its 'duct.' Probably the converging furrows found on the plicated extremity of the Fallopian tube may assist in directing the ovum to the *ostium abdominale*. If by chance the ovum be not caught and carried away to the uterus as described, it may fall into the peritoneal cavity and perish ; or if it has been already fertilised, abdominal fœtation may occur, the peritoneum acting as a matrix in which the embryo may develop. The method by which the ovum gains the Fallopian tube is not, however, settled. There is some evidence to show that it may be discharged into the abdominal cavity, and make its way into the Fallopian tube. The experimental introduction of small objects into the pelvic cavity has resulted in these being taken up by the tubes. In animals which have had one ovary removed the embryo has been found developed in the horn of the uterus on that side, though the ovum was derived from the opposite ovary. Even the ovary of one side and the uterine horn of the opposite side have been removed without interfering with conception. Notwithstanding, the simple direct method of Fallopian tube grasping the ovary appears the most reasonable explanation. In the dog special provision exists for the ovum to pass in this manner direct from the ovary into the Fallopian tube. As a result of the rupture of the Graafian follicle, a rent is made in the ovary. This wound fills with blood from the opened vessels, and for some time afterwards appears as a pigmented spot. If pregnancy has not supervened, it undergoes a retrogressive metamorphosis and soon disappears. If, however, the ovum is fecundated, the *corpus luteum*, as this pigmented spot is termed, continues to grow, and may be observed in the ovary even near 'term.'

The **Corpus Luteum** of the pregnant animal is very much larger than that of the non-pregnant, and it appears to be conclusively settled that the existence of this yellow tissue in the ovary is not merely for the purpose of filling up a cavity in its structure ; the yellow body is a ductless gland, which on pregnancy becomes an active secreting agent, producing a substance by which the ovum is anchored to the wall of the uterus, and its nourishment and development assisted. This ductless gland is functional until about the middle of pregnancy, when it is no longer a necessary factor in the nourishment of the embryo, and consequently degenerates. That the corpus luteum takes little or no share in the production of seasonal sexual excitement appears quite clear ; this is the function of the stroma of the ovary, which pours an internal secretion into the blood, and so brings about menstruation and œstrus.

The Cell.—It will help to a clearer understanding of the structure and development of the ovum if the features of body-cells in general are looked at.

There are two distinct classes of cell in the body. The more numerous tissue cells, known as *somatic* or *body cells*, are responsible for the structure of every tissue in the body, from the hardest to the softest. Another and much smaller set are the *germ cells*, which are solely concerned in the reproduction of the individual. The somatic cells are enormously active during embryonic life, and subsequently during the process of growth. When this is completed, they settle down to normal activity, which consists in growth by the process of division ; by this process of multiplying they are capable of repairing or replacing the worn-out cells of the body. The living animal is merely a gigantic collection of cells, each having an individual existence. As the cells die or are worn out, their places are taken by others, and this process is occurring from the moment the egg is impregnated to the death of the animal. Within this minute speck of material is contained all the elements of ife, and, small as it is, it contains all that is necessary for multiplying and producing its kind, in this respect differing in no essential particular from the larger organism of which it is only a microscopic atom.

All cells, somatic or germ, consist of cell-contents and cell-wall. The contents are colloidal in character, structureless, and are generally described as *protoplasm* or *cytoplasm*. Within the cell and lying in the cytoplasm is another and smaller cell, known as the *nucleus*. The nucleus consists of cell-wall and cell-contents, but the latter are not structureless. The nucleus of all cells is an

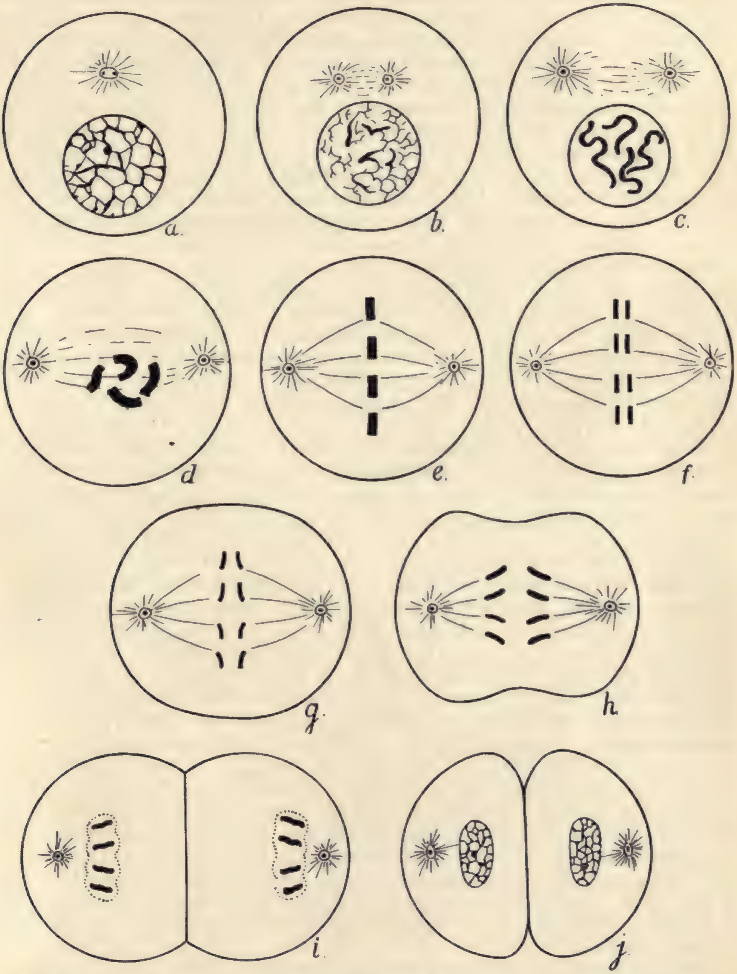

FIG. 244.—DIAGRAM ILLUSTRATING THE PROCESS OF CELL DIVISION (AFTER BOVERI).

important feature, without which the cell could not be reproduced. The reproductive material lies in the nucleus, seen to consist of a network of threads (Fig. 244, *a*), which, owing to their affinity for staining material, are known as *chromatin*. Within the threads are refractile bodies. In addition to the nucleus, the parent cell contains another and much smaller cell, known as the *centrosome*, a body of the utmost importance. The centrosome is surrounded by radiating fibrils, which give it the appearance of a star (Fig. 244, *a*), and the area surrounding it is spoken of as the *attraction sphere*. The reproduction of cells is brought about by indirect division, or *mitosis*, and the change is initiated in the nucleus. The chromatin threads of which this consists form larger threads by the process of fusion until the network is lost, and there only remains a collection of bodies resembling bent or curved rods (Fig. 244, *b*, *c*). These are the *chromosomes*, and the number present in each cell of the body is always definite for the particular species, but is not the same in all species of animals. There are, for example, twenty-four chromosomes in the mature somatic cells of man, the mouse, trout, salamander, and lily; in some of the threadworms there are two; in some of the crustacea as many as 168.* The number of chromosomes in the horse is twenty-six;† in the donkey twenty-four; in the cow sixteen. No matter what somatic cell is examined, the number is invariable for any given animal. The importance attached to the number, which is always even for every animal and plant sexually produced, will shortly be evident. The chromosomes themselves are of extraordinary interest.

The first change preparatory to the division of any cell takes place, as has been stated, in the nucleus, and while this is occurring the centrosome has divided into two, one passing to opposite sides of the nucleus (Fig. 244, *b*, *c*, *d*); these, with their star-like fibrils, are known as *astrospheres*. The chromosomes being formed, the cell wall of the nucleus disappears, and so liberates them (Fig. 244, *d*); they are then arranged between the two poles formed by the astrospheres, placing themselves end to end in Indian file equatorially (Fig. 244, *e*), and, having done this, they split longitudinally, and each forms two (Fig. 244, *f*). Each split chromosome is attracted towards the astrosphere nearest to it, so that an equal number of chromosomes pass to each of these bodies. The cytoplasm of the cell has hitherto been an inactive witness of this remarkable phenomenon. It now, however, divides into two portions (Fig. 244, *h*, *i*, *j*), each engulfing an astrosphere with its attendant chromosomes, and in this way two cells are made out of one, which resemble the parent in every respect, excepting that they only contain half the amount of chromatin, though the full number of chromosomes is present. The subsequent history of the new cell is simple. The chromosomes come together, form a reticulum, surround themselves with a membrane constituting the cell wall of the nucleus, and increase the amount of chromatin up to that originally existing in the parent cell.

Every animal originates from a cell which differs in no essential particulars from the one just described. The process of multiplication by which cells form a lion or a mouse, an elephant or mole, a philosopher or idiot, or a humble intestinal worm, are in all cases identical. In the development of the ovum the stages through which the higher animals have passed before they became higher may practically be witnessed or readily visualised. There is nothing in the early development of the ovum which sharply defines man formation from dog, cat, or pig formation ; each goes through the same phases up to a certain point, and then comes the parting of the ways. The unity of type of the embryo in its early stages is succeeded by its sharp differentiation ; this is even more remarkable than the incomprehensible starting-point.

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* 'Heredity and Disease,' by E. Le C. Lancaster, M.B., B.Ch., *British Medical Journal*, February 5, 1910.

† 'The Principles of Heredity applied to the Race-Horse,' by J. B. Robertson, M.R.C.V.S., 1910.

It is impossible in a work of this kind to enter more deeply into the physiology of the cell, or to relate the little which is known regarding it. It is obvious that a knowledge of the cell is intimately connected with the nature of life. All the physiological processes of the body considered in previous chapters are carried out by the cells, and the methods by which they work are chemical, physical, and biological problems of extraordinary difficulty.

Maturation of the Ovum.—The maturation of the ovum is not the same as its fertilisation. Maturation is concerned with the production of a perfect from an immature ovum, of a mature from an embryonic cell. This process is effected on the lines above indicated. It has been stated that the cells in the ovary at birth are imperfect ; their number is laid down, and this we have seen amounts to several thousands. They are completed as required, and are only matured some months or years after birth, depending on the species of animal. It is obvious that only a few are matured at one time, and, again, the species of animal determines whether they are matured, as in the woman, at short regular intervals or at relatively long intervals. The periodical development of a mature egg or eggs constitutes the essential feature of maturation.

The primitive ovum takes its first step towards maturation by the process of cell division. Two cells unequal in size result : one is still the ovum, the other the *first polar body*. The number of chromosomes in the immature ovum was originally, in the case of the mare, twenty-six ; as the result of the formation of the first polar body, these twenty-six fuse and form thirteen. Before the first polar body is cut adrift the thirteen chromosomes split, so that thirteen go to the polar body and thirteen remain with the ovum. Though these two cells contain only half the number of chromosomes contained by a somatic cell, yet each is a whole chromosome, and not half a one, as in the division of somatic cells. The ovum next divides a second time, and extrudes a *second polar body*. This time the thirteen chromosomes either split or divide, thus forming twenty-six ; half pass to the second polar body, and half remain with the parent cell, the ovum. So that the formation of the two polar bodies has caused the ovum to suffer a loss in the number of chromosomes, and it is finally only left with half its original number; but its cytoplasm has undergone no practical loss. The polar bodies are regarded as abortive ova; they die, and are not concerned in the subsequent changes. The important point is that the mature ovum is left with only half the number of chromosomes normal to the cells of the species. One further change in the process of maturation has also taken place, and that is the centrosome of the cell is lost. These remarkable changes pave the way to an understanding of what follows, should impregnation of the ovum occur.

An ovum without a centrosome and with only half the normal number of chromosomes has, in order to be fertilised, to be furnished with a centrosome and its full number of chromosomes. It is the function of the spermatozoon to supply these.

Maturation of the Spermatozoa.—The cells of the immature spermatozoa also undergo a process of ripening. The immature spermatozoon is known as a *spermatocyte.* As the result of cell division it forms two secondary spermatocytes; both of these undergo a further division and form four *spermatids.* The four spermatids furnish four mature *spermatozoa.* There are no abortive spermatozoa formed, as there are abortive ova. At each cell division in the above stages, the number of chromosomes contained in the nucleus in the head of the spermatozoon undergo a reduction, until the mature spermatozoon, in the same way as the mature ovum, only possesses half the number of chromosomes. When the spermatozoon impregnates the ovum, it brings to it the important centrosome and a nucleus. This nucleus provides the ovum with the chromosomes of which it was short. In the ass the number of chromosomes is twenty-four, and Robertson* explains the infertility of mules on the ground that there is an odd number of chromosomes in their cells—*i.e.*, twelve derived from the ass and thirteen derived from the horse, or a total of twenty-five.

In the present light of knowledge the interest attached to chromosomes is considerable. The chromosomes, according to modern thought, convey the hereditary characters of the transmitters, so that the resulting embryo has its characteristics implanted at the time of conception, in theory half being derived from each parent.

Ovulation is the process of egg extrusion. In some animals, as the rabbit and ferret, it can only occur as the result of coition, the presence of spermatozoa in the uterus being essential to the act. In others—and they represent the majority—such as the mare, donkey, cow, sheep, pig, and dog, ovulation occurs during œstrus, but the act of copulation is not necessary to extrusion, and in such animals artificial insemination is therefore possible. The period of œstrus is not necessarily identical with the period of ovulation ; œstrus may occur without ovulation, and ovulation may occur without œstrus. Ewart says the mare may mature and discharge one or more eggs after she has become impregnated. Ovulation occurs at the moment the Graafian vesicle ruptures and the ovum is ejected. The number of ova which may be extruded during one sexual period is not known with any degree of certainty ; in the case of the cat and dog there is evidence of several being ejected, for each fœtus represents a separate egg. The number of eggs laid is always greatly in excess of the number impregnated, and the mare, which probably only produces one egg at a time, and with whom twin births are very rare, is believed by Ewart to shed about ten or twenty ova annually. Whether an equal number is discharged by each ovary is unknown. Probably one ovum for the mare, cow, ass, deer, elephant, or monkey, at each œstrous period is the rule, though two may be discharged. The sheep probably discharges one to four ; the dog, wolf, and cat five to six ; the pig ten. or even fifteen.

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* *Op. cit.*

Fertilisation of the Ovum.—Somewhere in the Fallopian tube, though occasionally on the surface of the ovary, the meeting between the sperm and germ cell occurs. The wriggling movements of the sperm cell in the Fallopian tubes propel the spermatozoa towards the ovary. The lashing of the cilia in the tube assists the passage of the ovum towards the uterus. There is no explanation of how the spermatozoa find their way into those minute pin-point holes which represent the uterine end of the Fallopian tubes. The spermatozoa meet the egg ; owing to the enormous number existing even in a droplet of the secretion, it is easy to understand why the ovum cannot escape coming in contact with them. A single spermatozoon penetrates the wall of the ovum, and enters the cytoplasm. Others may attempt to follow, but the surface of the egg at once becomes impervious to further attacks. The spermatozoon having got inside the egg, and lying in its cytoplasm, loses its tail, which is no longer required. The essential portion of the organism is the head and middle piece. The former is the cell with its nucleus, which contains the all-important chromosomes ; the middle piece contains the centrosome, which, it will be remembered, was lost to the mature ovum. There are now two nuclei within the egg, one the male, the other the female *pronucleus*. These meet, fuse, and, under the direction of the centrosome, the process of cell division immediately follows their fusion. The union of these two nuclei is a matter of extraordinary importance. It will be remembered that by a process of reduction the chromosomes in the ovum and spermatozoon were reduced in each case to one half. On the union of the nuclei, the full number peculiar to the species is created, each nucleus bringing in half, and as the result of this a *segmentation nucleus* is formed. From this segmentation nucleus the future animal is formed. The segmentation nucleus now divides, the chromosomes it contains *split*, so that each division contains the number of chromosomes normal to the species, the chromosomes of each parent being represented in each division of the cell, and in each subsequent subdivision. It is believed that every cell from which the embryo originates obtains maternal and paternal chromosomes.

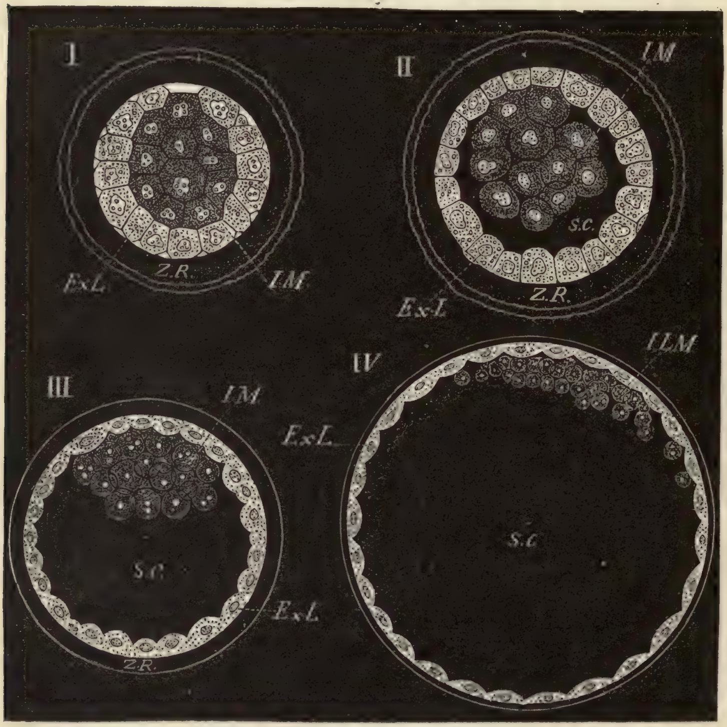

FIG. 245.—SECTION OF A RABBIT'S OVUM AT THE CLOSE OF SEGMENTATION. II., III., IV., STAGES IN THE FORMATION OF THE BLASTODERMIC VESICLE (E. VON BENEDEN).

Z.R., Zona radiata; *Ex.L.*, external layer of cells; *I.M.*, inner mass of cells; *I.L.M.*, Inner lenticular mass of cells; *s.c.*, segmentation cavity.

It will be observed that the spermatozoon and ovum are the complement of each other. The ovum contains an abundance of cytoplasm and a nucleus, but no centrosome; the spermatozoon contains no cytoplasm, but both nucleus and centrosome; the ground common to the two is that they both contain the same number of chromosomes. There is a great deal of recent experimental work which tends to show that, if to the ovum a centrosome be supplied, or to the spermatozoon some cytoplasm is given, both may then develop into an ovum without coming together. This remarkable fact has been proved to occur in the eggs of the sea-urchin.

When segmentation of the ovum is completed, as indicated in Fig. 245 I., a sphere is formed (Fig. 245, IV.), consisting of an outer cellular layer, formed of single cells (*Ex. L.*), enclosing a cavity known as the *segmentation cavity* (*s.c.*). The sphere is called the *blastodermic vesicle*. It contains broken-down yolk, and at one part some smaller cells (*I.L.M.*), which probably spread over the inner wall of the sphere and form an inner cellular layer. The outer cellular layer is the *epiblast;* the inner cellular layer is the hypoblast. While the latter is spreading over the inner wall, a white disc is developed at one point of the

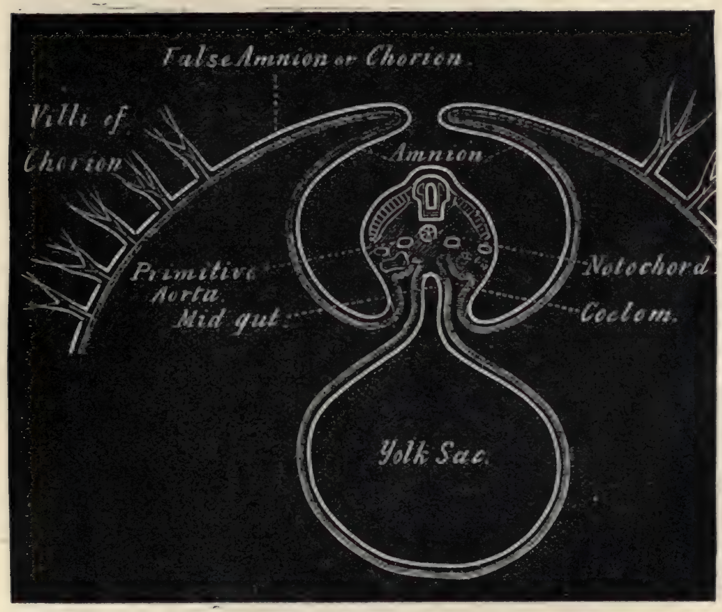

FIG. 246.—DIAGRAM OF A TRANSVERSE SECTION OF A MAMMALIAN EMBRYO, SHOWING THE MODE OF FORMATION OF THE AMNION (SCHÄFER).

The amnion folds have nearly united in the middle line.

vesicle; this disc is the *germinal area.* In this area the embryo develops. A development of the cells of the epiblast leads to the formation of a groove in the area, known as the *primitive groove;* the sides of the groove grow up, meet, and enclose a space, the *neural arch*, and from this arises the cerebro-spinal system. A third layer of cells now develops between the epiblast and hypoblast, and is spoken of as the *mesoblast.*

The mesoblast furnishes a layer of cells under the neural canal, the *notochord* (Fig. 246); from these the bodies of the vertebræ develop. The mesoblast splits: the outer layer of it unites with the epiblast, and so forms the *somatopleure;* the inner unites with the hypoblast, and forms the *splanchnopleure.* As the result of the splitting, a cavity is formed between the layers, known as the *pleuro-peritoneal space*, or *cœlom* (Fig. 246). This is the body cavity of the future embryo. From the three layers of cells developed around the ovum the following tissues of the embryo are formed:

From the Epiblast:
- The whole of the nervous system, both cerebro-spinal and sympathetic.
- The epithelial sensory end-organs of the nerves of special sense, and the crystalline lens.
- The epidermis and its appendages—hair, hoof, claws, horns.
- The epithelium of all glands opening on the surface of the skin, including mammary, sweat, and sebaceous.
- The epithelium of the mouth (not the tongue) and glands opening into it, the enamel of the teeth, and the epithelium of the anus.
- The epithelium of the nasal passages and facial sinuses.

From the Mesoblast:
- The bones, cartilages, and connective tissues of the entire body.
- The whole of the muscles, skeletal and visceral.
- The entire vascular and lymphatic system—blood-corpuscles, spleen, and serous membranes.
- The generative organs and generative elements.
- The urinary organs.

From the Hypoblast:
- The epithelium of the alimentary canal and the ducts of all glands opening into it.
- The epithelium of the respiratory organs.
- The cells of the liver and pancreas.
- The epithelium of the bladder, ureters, thyroid body, and part of thymus gland.

During the growth of the mesoblast the embryo, which is developing in the germinal area, is gradually being lifted off the blastodermic vesicle by the formation of a sulcus or depression which extends around the embryo. The embryo at this period possesses within it two tubes—one dorsal (the neural canal), the other ventral (the alimentary canal). The latter opens in front and communicates with the yolk sac (Fig. 247), and between the two is the mesoblast.

Nutrition of the Embryo.—The development of the embryo need not be described beyond this point; what has been introduced of the subject is to illustrate the important features of the source of the various body tissues, and the method by which the early embryo is nourished. Up to the seventh week in the embryo of the mare the nourishment is entirely carried out by the **yolk sac**. This structure may persist after completing its function, as in the case of the dog. The nourishment contained in the yolk sac of the mammal is not true yolk, but uterine milk derived from crypts in the wall of the uterus.

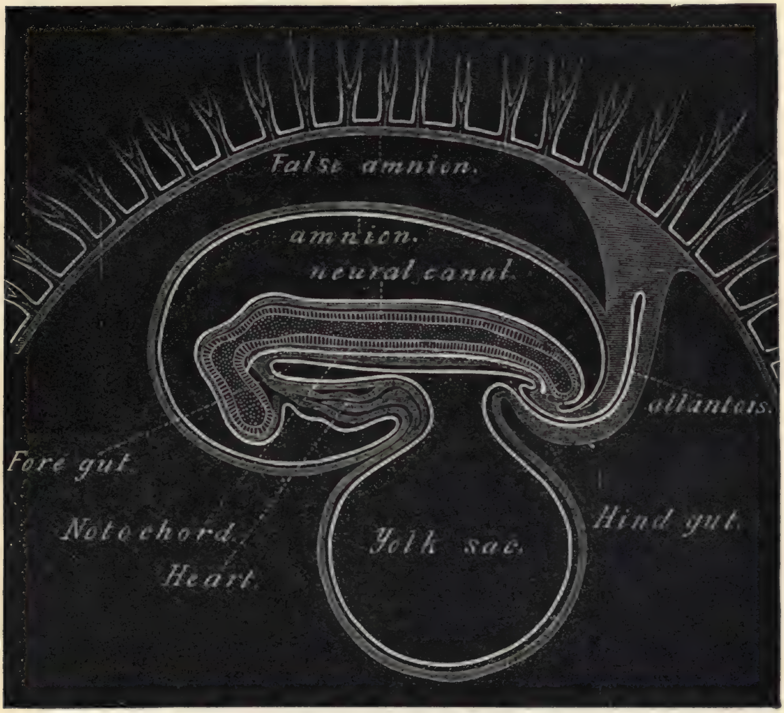

FIG. 247.—DIAGRAM OF A LONGITUDINAL SECTION OF A MAMMALIAN OVUM, AFTER THE COMPLETION OF THE AMNION (SCHÄFER).

When the yolk sac is exhausted, the nutrition of the embryo is otherwise provided for—*e.g.*, it is brought into communication with the blood of the mother, and the blood circulating through her system is indirectly brought into contact with the blood in the vessels of the embryo, through the medium of a vascular sac in which it is lying. The growth and development of the coverings of the embryo must now be looked at.

The Decidua.—At every monthly period in the human female the mucous lining of the uterus undergoes certain changes, which result in the formation of a membrane known as the *decidua ;* this is in shape a counterpart of the interior of the uterus. The membrane is shed during menstruation ; if the woman becomes pregnant the decidua is not exfoliated, but undergoes further development in connection with the ovum. The latter on its arrival in the uterus becomes embedded in the folds of mucous membrane which grow up around and anchor it to the wall of the uterus. That portion of the mucous membrane which grows over and envelops the ovum is known as the *decidua reflexa*, that which lines the interior of the uterus is known as the *decidua vera*. Through the decidua vera the uterine glands grow, and later on in embryonic life, when the final circulation is established between the fœtus and the mother by means of the *placenta*, the latter on the maternal side is attached to a portion of the decidua vera, and to this part the term *decidua serotina* is given. After the birth of the child, the membrane covering it, the placenta, and the uterine decidua, are all cast off, with the result that the interior of the uterus is converted into a large raw wound.

Placenta.—No domesticated animal has a decidua ; the ovum is attached in quite another way to the uterine wall, and, though a placenta exists, it is differently arranged to that of the human female. This has led to the primary classification of placentæ into *deciduate* and *non-deciduate*, but these terms, in the light of recent inquiry, are not appropriate, for it is no longer a matter of importance from a morphological point of view whether a portion of the maternal tissue comes away with the afterbirth or not. Assheton* proposes to group placentæ into two great types, *placenta cumulata* and *placenta plicata*, these terms being based on the arrangement of a certain group of cells (the *trophoblast*) in the outer layer of the embryo, through which the embryo is secured to the wall of the uterus. Whatever form the placenta may be, or whatever the attachment between the fœtus and the mother, it is always originated by the trophoblast cells. In the cumulate type of placenta the trophoblast cells heap themselves up and *destroy the uterine epithelium*, and form spaces into which the maternal blood escapes ; while in the plicate there is no heaping up, but a process of folding and ingrowth takes place, *the uterine epithelium in most cases being left intact*. The pig is the extreme type of plicate placenta ; then follows the mare, cow, sheep, while the placenta of man and carnivora is of the cumulate type. It must not be supposed that these types are sharply divided ; for instance, the sheep has a plicate placenta which contains cumulate features, and the placenta of the dog, though cumulate, has features of a plicate type.

Besides recognising placentæ as deciduate and non-deciduate, or plicate and cumulate, they are further classified according to the disposition of the chorionic villi. If the villi are scattered over the whole surface of the chorion, the placenta is *diffuse*, as seen in the sow, mare, and camel. The only parts of the chorion in these animals destitute of villi are the poles, and the smooth patch is very minute. If the villi are gathered into tufts upon the surface of the chorion, and these tufts correspond to elevations of the mucous membrane of the uterus, the placenta is *cotyledonary* or *polycotyledonary*. The tufts and elevations are the fœtal and maternal cotyledons respectively, and number sixty, more or less. If the villi are disposed in a strap-like manner around the envelopes, leaving the poles for some distance free from villi, the placenta is *zonary*, and such a condition is found in the placenta of the dog and cat. In the rabbit and woman the placenta, from its shape, is discoidal or metadiscoidal.

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* 'On the Morphology of the Ungulate Placenta,' by R. Assheton, M.A., *Phil. Trans.*, B, vol. cxcviii., 1905.

Fœtal Membranes.—If the egg of the hen be examined after incubating nine days, the appearance seen in Fig. 248 presents itself. A chick in an advanced stage of development is bound within a thin tough skin, containing fluid; this water-jacket is known as the *amnion*, and its use is to prevent jar when the egg is moved. An identical arrangement exists in mammals. The supply of food required by the embryo chick during development is contained in the *yolk sac*; to this food-supply the embryo is connected by a stalk through which the nourishment enters its body. The walls of the yolk sac are vascular and connected with the vessels of the embryo. It is through the medium of the vascular wall that the altered yolk is taken up. The modified yolk sac is found in mammals (Figs. 246, 247). It does not contain yolk, but takes up the nourishment secreted by the uterine glands, and for a time this suffices for the needs of the embryo. The chick has another fœtal appendage known as the *allantois*;

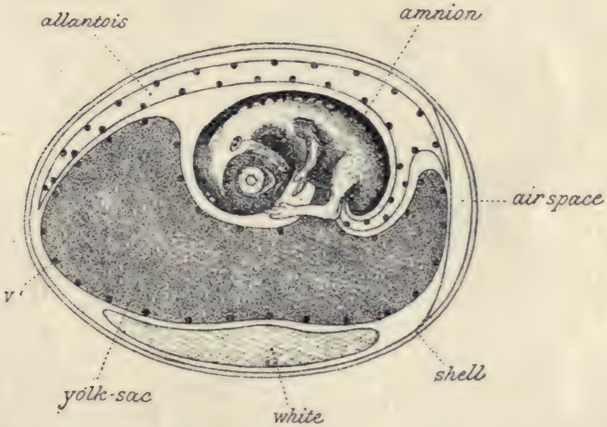

FIG. 248.—HEN'S EGG AT THE NINTH DAY OF INCUBATION (EWART AFTER MILNES MARSHALL).

it grows out from the body, being connected to the embryo by means of a stalk, and forms a vascular sac through which blood from the chick's body circulates. The allantois in the chick is a breathing organ ; the air enters through the pores of the shell, and the blood takes up oxygen from the air surrounding the allantoic sac ; an air space also exists at the end of the shell. An allantois exists in the mammal (Figs. 247, 249) ; unlike that of the bird, it does not obtain oxygen from the air, though it is a breathing organ in the sense that it furnishes oxygen to the fœtus.

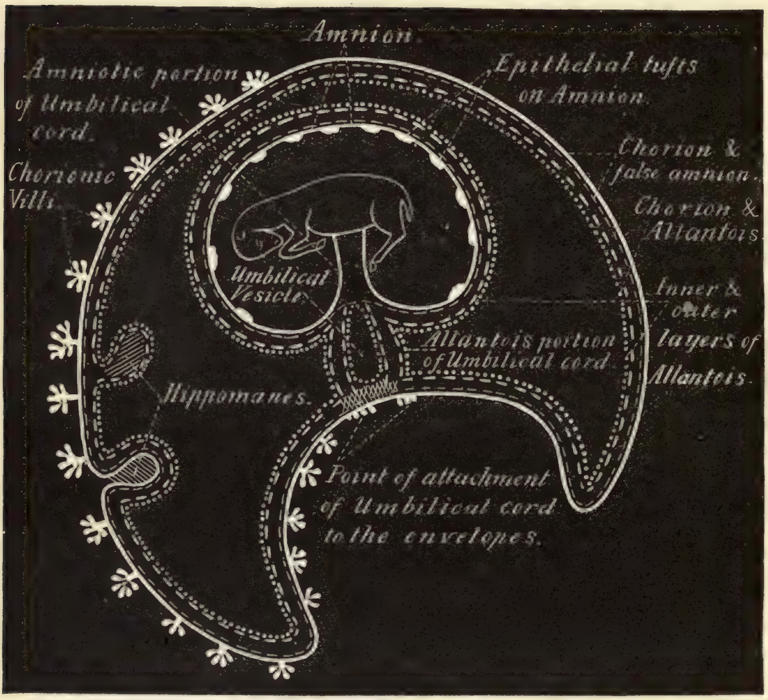
Amnion.
Amniotic portion of Umbilical cord.
Epithelial tufts on Amnion.
Chorion & false amnion.
Chorionic Villi.
Chorion & Allantois
Umbilical Vesicle.
Inner & outer layers of Allantois.
Allantois portion of Umbilical cord.
Hippomanes.
Point of attachment of Umbilical cord to the envelopes.

FIG. 249.—DIAGRAM OF THE FŒTAL ENVELOPES OF A FIVE MONTHS HORSE EMBRYO (BONNET).

Immediately enveloping the mammalian embryo is the **amnion.** This arises from the same portion of the embryo which gives origin to the body wall, through ridges which grow up over it (Figs. 246, 249), and eventually form a sac. This sac contains a fluid in which the fœtus lives. The fluid, or **liquor amnii,** is alkaline in reaction, and yellowish in colour during the early days of gestation, but reddish towards the end of it, probably due to discoloration with fœtal fæces, or *meconium*. The amniotic fluid contains proteins, mucin, urea, sugar, lactic acid, keratin, and some salts. Besides these there are also portions of hoof, epithelium, etc., derived from the fœtus. The source of this fluid is probably by transudation from both the fœtus and mother. Indigo blue injected into the vessels of the mother tinges the amniotic fluid, though it does not stain the fœtal tissues. The function of the amniotic fluid is protective to mother and fœtus. The latter lies on it as on a water-bed, and during parturition it assists in dilating the os and lubricating the maternal passage.

The **Allantois** grows out from the body of the embryo at the future umbilicus. The part within the body forms the bladder, that outside it forms a sac which, in the mare, completely envelops the amnion (Fig. 249), but in ruminants only partly so (Fig. 250). The bladder and the cavity of the allantois are connected by a funnel-shaped canal in the umbilical cord known as the **urachus.** The remains of this may be seen in the adult as a scar on the fundus of the organ. The fluid found in the allantois is derived from the fœtal urine. In the first instance it is colourless or turbid, later on it becomes brown in tint. This fluid contains urea and a substance allied to it, allantoin, also albumin, sugar, lactic acid, and certain salts. The allantois is the organ of respiration, and to a limited extent of nutrition. During early fœtal life the vascular wall of the allantois is able to bring the blood of the embryo sufficiently near to that of the uterus to effect an exchange of gases. Later on, as we shall see (p. 716), it furnishes the villi which penetrate into the walls of the uterus through the chorion.

Floating in the allantoic fluid of the mare, or attached to the wall of the sac, are certain peculiar masses termed **hippomanes** ; their origin and use are quite unknown. It is usually considered that these bodies, which may be multiple, are found in the foal's mouth at birth, but we are assured* that this is a fallacy. Further, these bodies are contained in the allantois sac, whereas the fœtus lives in the amnion. Hippomanes have also been observed in the cow.†

The **Chorion** envelops the two previous coverings. Through the umbilical cord it forms the vascular connection between the fœtus and the mother, while the villi on its surface project themselves into the mucous membrane of the uterus, not through the medium of a decidua, as in the woman, but directly into the

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* Mr. T. B. Goodall, F.R.C.V.S., Christchurch.

† It is a curious fact that even at the present day, in some country districts, hippomanes are sought for in virtue of the properties they have been supposed to possess from time immemorial—viz., for use as love philtres.

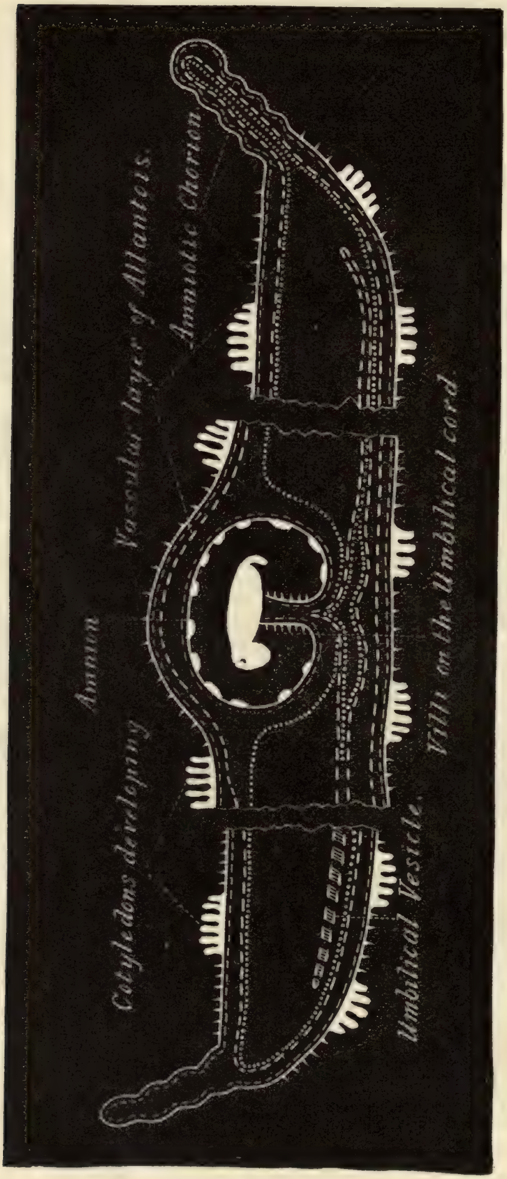
Amniotic Chorion
Vascular layer of Allantois
Amnion
Cotyledons developing
Villi on the Umbilical cord
Umbilical Vesicle

FIG. 250.—DIAGRAM OF THE FŒTAL ENVELOPES OF RUMINANTS (BONNET).
Only the central portion and extremities are represented.

uterine wall. The bloodvessels of the chorion and those of the uterus do not anastomose, but the fœtal villi, which project into sinuses in the uterus, are bathed in the blood these contain, and in this way, through the endothelial lining of the vessels of mother and embryo, the blood of the fœtus receives oxygen and gets rid of carbon dioxide.

Umbilical Cord.—After the formation of the fœtal envelopes the body walls rapidly close in, the splanchnopleure being received up into the body to form the primitive gut and its derivatives, the somatopleure forming the body wall and the limbs. The embryo or fœtus maintains its connections with the placenta by means of the umbilical cord. This is composed of structures connected with the amnion and the body wall at the umbilicus; of others in connection with the allantois and the urachus, and with these the umbilical arteries and vein, or veins (ruminants). All are cemented together by an embryonic connective tissue, the Whartonian jelly.

Determination of Sex.—Heape* maintains that there is no such thing as a pure male or female animal, but that all contain a dominant and a recessive sex, excepting hermaphrodites, in which both sexes are equally represented. The assumption of male characteristics in old females, and of female characteristics in old males, of the human species is noted by Heape. We have referred on p. 692 to the remarkable effect of castration and ovariectomy on the skull of young cats, castration producing a female skull, ovariectomy a skull of the male type. Caponing also induces female plumage. Injuries of the ovaries in birds, as previously stated, are associated with crowing and male plumage—all of which is evidence that the recessive sex asserts itself when the dominant sex becomes impaired, and supports the view held by Heape and others that there is no such thing as a pure male or female animal. If this be true, it naturally follows that a male ovum is fertilised by a female spermatozoon, and a female ovum by a male spermatozoon (Heape). Everything, in fact, points to ova and spermatozoa being sexual—that is to say, there are male and female ova, male and female spermatozoa. Microscopic differences in the structure of spermatozoa have also been observed, which have led to their classification into two groups, which are, in all probability, male and female.

The bearing of Heape's work on the determination of sex is of great importance. He maintains that the sex of the offspring is fixed at the time of fertilisation, and that no influence exerted subsequently can alter it. This is opposed to popular ideas, but results from an acceptance of the hypothesis that an ovum in which one sex is dominant must be fertilised by a spermatozoon in which the opposite sex is dominant; whether the sex be determined by the ovum or spermatozoon depends upon which is the more powerful of the two. Heape's study of the ovary of the rabbit† shows that ova may degenerate, and that one of the chief causes is nutrition. He is of opinion that nutrition has a selective action on ovarian ova, and so effects a variation in the proportion of the sexes of the ova produced. Where no such selective action occurs in the ovary, the proportion of the sexes of ovarian ova produced is governed by the laws of heredity.

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* 'Notes on the Proportion of Sexes in Dogs,' by W. Heape, M.A., F.R.S., *Proceedings of the Cambridge Philosophical Society*, vol. xiv., part. ii., 1907.

† 'Ovulation and Degeneration of Ova in the Rabbit,' *Proceedings of the Royal Society*, B, vol., lxxvi. 1905.

Twin and Multiple Births.—As a rule, only one embryo results from the fertilisation of a single egg, but occasionally two develop, and in this case the fœtal membranes are common to both. Twin births, however, more commonly arise from the fertilisation of two eggs; in the case of multiple births there is no doubt that each embryo is the result of the impregnation of a separate ovum.

Twin births resulting from the impregnation of a *single* egg are found to occur in cattle, and the offspring generally consists of a potent bull calf and so-called heifer calf, the latter being sterile and known as a **free-martin.** The nature of a free-martin has been a developmental problem for one hundred and fifty years. John Hunter drew attention to it and preserved the parts, which, in the light of present knowledge, have recently been re-examined.* To Berry Hart we are indebted for a solution of the problem. He points out that as in the free-martin two embryos arise from a single egg, the genitals of each have to be provided from a single cell, which normally might give rise to one perfect male. Instead of two perfect males resulting, one perfect and one imperfect follows, for the free-martin, though generally resembling the female externally, is in reality an imperfectly developed *male.* The external part of the genital tract is like that of the cow, but the inner part is defective, there being a very rudimentary vagina and a knob of uterus, with testes and Wolffian bodies imperfectly developed. Hart, in his monograph, points out that there are female as well as male free-martins, but they are very rare. A free-martin co-twin with a male is a male, a free-martin co-twin with a female is a female. The most frequent variety is the male—viz., a potent bull born co-twin with an apparent heifer which is sterile. In all cases one animal is potent, the other sterile. It has been usual to regard free-martins as a form of hermaphrodism, but embryologists have established that an hermaphrodite must possess both male and female sexual organs, and this is not the case in a free-martin.

Implantation of the Ovum.—In the **sheep**† the impregnated egg enters the uterus on the fourth or fifth day, and travels slowly along it until the ninth day. On the ninth day the zona radiata ruptures, and the *blastocyst* (that is, the external cover of the cellular mass) lies in contact with the uterine epithelium. On the twelfth day the ovum has reached nearly to the lower limit of the horn in which it lies, the glands of the uterus enlarge, and the blastocyst rapidly elongates so that each end grows out to the tip of each horn of the uterus. If one embryo only be present, it extends through both horns of the uterus ; if there are two, they are each confined to one horn. On the seventeenth and eighteenth day the first attachment of the embryo to the uterus is effected, a very important period in embryonic life. Up to this time the only nourishment available, exclusive of the yolk sac, is that furnished by the juices poured into the uterine cavity by the glands, and until the twentieth day the ovum receives no other source of supply but this. On the twenty-eighth day *villi* on the external covering of the embryo are well developed, and on the maternal cotyledons are little depressions, into which they fit. The *allantois* has grown rapidly, and the *yolk sac* has become reduced as the allantois increases. By the forty-fourth day the fœtal cotyledons are scattered over the whole surface of the embryonic covering. On the seventy-eighth day the general character of the placenta is established. As the uterus swells, owing to the increase in size of its contents, it does so generally excepting the upper part of the horns, which are but little longer than normal, and are engaged in active secretion.

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* 'The Structure of the Reproductive Organs in the Free-Martin,' by D. Berry Hart, M.D., *Proceedings of the Royal Society of Edinburgh,* vol. xxx., part iii.

† 'The Morphology of the Ungulate Placenta,' by R. Assheton, M.A., whom, in the above account of the sheep, we have entirely followed (*Phil. Trans.,* B, vol. cxcviii., 1905).

This condensed account from Assheton of the development of the embryo of the sheep is the first exact knowledge of how the embryo of a ruminant comports itself during the early days of development.

The implantation of the embryo of the **horse** has been dealt with by Ewart,* not with the same degree of fulness as the above, as that is practically impossible, but sufficiently so to show not only the characteristic features of the process, but their profound practical bearing on the hygienic care of brood mares.

The human decidua grows over the ovum on its arrival in the uterus, and so prevents its escape (see p. 708). No such pouch is formed in the ungulates, and the escape of the ovum before it is securely fixed to the wall of the uterus is not unlikely, especially in the horse, where the connection between the embryonic sac and the uterus is easily broken down. To understand how this occurs, Ewart points out that the remote ancestors of the horse were probably born on the forty-seventh or forty-eighth day of conception, and, like the ancient and primitive mammals, the opossum and kangaroo, passed from the uterus to a pouch, where they lay securely suspended by a teat until their perfect development was completed. The arrangement by which the equine embryo is anchored, as Ewart calls it, to the wall of the uterus is in the first instance by some of the cells of the outer layer of the embryo, at a part which is in communication with the yolk sac. This connection (Fig. 251, *a*, *b*, *c*) is of a very slender kind, and is the only one which exists up to the fifth week. At the fifth week additional means of securing the embryo to the wall are evident by an increase in the size and strength of the original yolk-sac adhesion. There is also a girdle about ¼ inch wide, not hitherto found in any mammal (Ewart), placed around the equator of the embryo (Fig. 251, *t.g.*). This girdle obtains adhesion to the uterine wall, and so strengthens the original anchorage. About the end of the sixth week the attachment of embryo to uterus is again becoming precarious, for the yolk-sac attachment area has become less (Fig. 252, *a-c*), while the girdle has shifted from the equator to near the pole (Fig. 252, *t.g.*). At this period Ewart considers the primitive ancestors of the horse were born.

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* 'A Critical Period in the Development of the Horse,' by T. C. Ewart, M.D., F.R.S., 1897.

At the end of the seventh week the supply of nourishment through the medium of the yolk sac has nearly come to an end, the absorbing area next the uterus is considerably reduced, and it is at this period that an entirely new source of supply and attachment has to be found. The supply is furnished by means of the *allantois*, while the additional attachment is furnished by the girdle becoming folded into ridges, which fit into grooves and depressions in the mucous membrane of the uterus. The outer cover of the embryo beyond the girdle is dotted with numerous minute points, which subsequently become villi; the villi are derived from a sprouting of the allantoic sac, and as they grow are accommodated in pits in the uterine wall. By the end of the eighth week this has been accomplished. The villi are not more than ⅛ inch long, even when full grown, and at birth they are withdrawn from the uterine pits. Once the villi have become established, the question of nourishment becomes no longer a difficulty, and the critical stage in the development of the horse is passed.

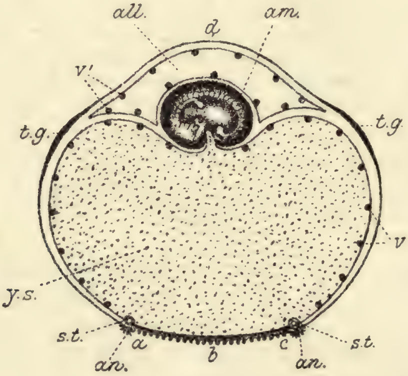

FIG. 251.—SEMI-DIAGRAMMATIC REPRESENTATION OF A FOUR WEEKS HORSE EMBRYO AND ITS FŒTAL APPENDAGES, NATURAL SIZE (EWART).

am., The amnion; *y.s.*, the yolk sac, which is vascular (*v*) as far as the circular bloodvessel (*s.t.*), and crowded with granules which have entered by the absorbing area (*a*, *b*, *c*) of the yolk placenta; *all.*, the allantois. The embryo measures nearly ⅜ inch in length, and is curved so that the tail lies against the head.

The cause of mares 'breaking service' from the sixth to the ninth week is explained by Ewart in the light of his inquiries. At the third, sixth, and ninth week the physiological changes associated with œstrus are likely to supervene and shake the reproductive system. At the third week the risk of casting off the embryo is not so great, as the area by which it is attached to the uterine wall is sufficiently large to render it moderately secure, but at the sixth week a change from yolk sac to placental nourishment is being effected and the yolk-sac area is less than it was at the third week. At such a time a contraction of the uterine horn will be followed by expulsion of the embryo. At the ninth week the question of not 'breaking service' depends on whether the villi have appeared in time, and obtained a sufficiently intimate relation with the uterine vessels to supply the embryo with the additional nourishment its development requires, that through the yolk sac being insufficient.

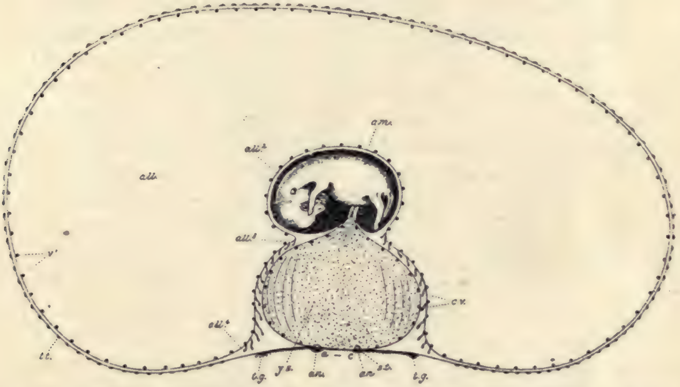

Fig. 252.—A Seven Weeks Horse Embryo, Half Natural Size (Ewart).

all., Allantois ; *am.*, amnion ; *c.v.*, non-vascular villi between the allantois and the yolk sac, not hitherto found in any mammal, and function unknown ; *y.s.*, yolk sac ; *a-c*, absorbing area of the yolk placenta ; v^1, vascular villi of allantois ; *t.t.*, external vascular villi over the surface of the embryonic sac.

Ewart says that the embryo of the mare usually occupies the right horn of the uterus, and in the early days is suspended by the yolk sac from the upper wall of the organ, the head being towards the body of the womb. Later the fœtus may lie in the body of the uterus, but the hind-limbs remain to the last in the right horn.

Fœtal Circulation.—With the formation of the fœtal envelopes and the development of the heart, the circulation takes on a course altogether different from that in the vascular area in early embryonic life. The placenta acts as the fœtal respiratory and food-absorbing organ. Impure blood that has circulated through the tissues of the developing young is brought to the placenta by the umbilical arteries, these acting to the fœtus as the pulmonary arteries to the adult. After an interchange of gases and a renewal of food supply, the blood is carried away to the fœtus by means of the umbilical vein, or veins, found in the cord. The vein enters the body at the navel or umbilicus, passes forward along the floor of the abdomen, reaches the falciform ligament of the liver, travels along the free edge of that structure, and empties itself into the portal vein. After birth the remains of the umbilical vein are found as a thickening at the free edge of the falciform ligament, and form the round ligament of the liver. In ruminants the umbilical veins are two in number, but they unite to form a single vessel on entering the body. The vessel thus formed passes along the abdominal floor towards the falciform ligament to occupy the same position as in other animals, but before reaching it, it detaches a large branch, the *ductus venosus* (Fig. 253, *d.v.*), which passes upwards to join the posterior vena cava. After the blood has circulated in the liver it leaves by the hepatic trunks, and is poured into the posterior vena cava, where it meets with the blood in that vessel, and is thus conducted to the heart. In the horse the whole of the fœtal blood passes via the portal vein through the liver before reaching the heart. In ruminants, part of the blood passes through the liver, and part goes direct to the systemic circulation of the fœtus through the ductus venosus.

In the fœtal heart the cavities of the right and left auricles are in communication by means of a foramen, the *foramen ovale.* This opening in many animals is provided with a valve, the Eustachian, that stretches from the mouth of the posterior vena cava to the annulus or thickened border of the foramen ovale ; it is absent from the heart of the fœtal horse and pig. The function of this valve is to direct the blood-stream into the left auricle ; the blood in this way gets into the left auricle, passes into the left ventricle, and thence into the aorta. The greater portion is driven into the vessels that supply the head, neck, and fore-limbs (anterior aorta and branches), and is conveyed to the head and anterior portion of the body ; the remainder passes backwards in the posterior aorta. The head, it will be noticed, receives almost pure blood. After the fluid has circulated in this part of the body, it is returned to the right auricle of the heart by the anterior vena cava. From the right auricle it passes to the right ventricle, and from this cavity it is pumped into the pulmonary artery. The lungs, however, are not functional, and are more or less solid organs ; consequently

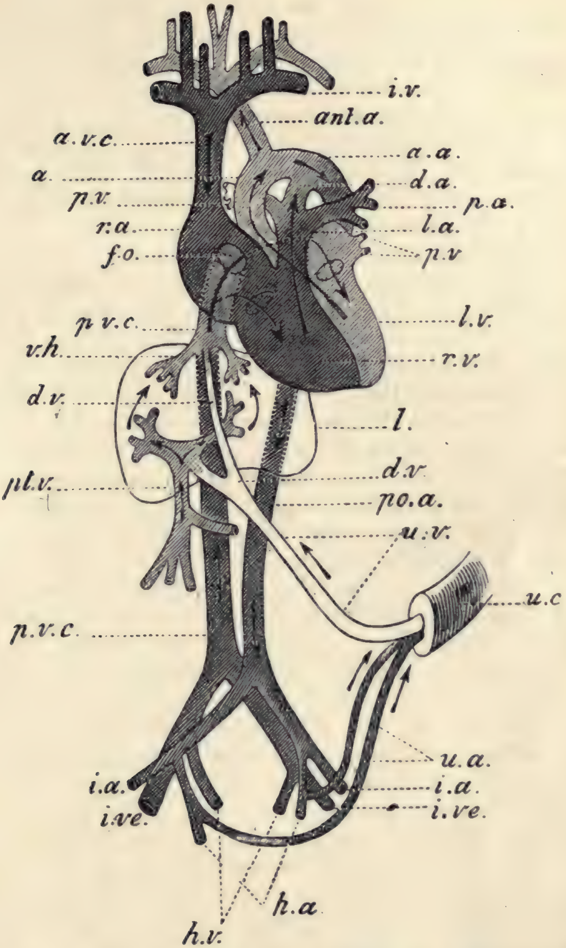

FIG. 253.—DIAGRAM OF THE FŒTAL CIRCULATION (ELLENBERGER).

u.v., Umbilical vein; ***d.v.***, ductus venosus; ***pt.v.***, portal vein; ***l.***, liver; ***v.h.***, hepatic veins; ***p.v.c.***, posterior vena cava; ***r.a.***, right auricle; ***f.o.***, foramen ovale; ***r.v.***, right ventricle; ***p.a.***, pulmonary artery; ***d.a.***, ductus arteriosus; ***l.a.***, left auricle; ***l.v.***, left ventricle; ***a.***, the aorta; ***a.a.***, arch of aorta; ***ant.a.***, anterior aorta; ***i.v.***, innominate veins; ***a.v.c.***, anterior vena cava; ***po.a.***, posterior aorta; ***i.a.***, iliac artery; ***h.a.***, hypogastric artery; ***u.a.***, umbilical arteries; ***i.ve.***, iliac veins; ***h.v.***, hypogastric veins; ***u.c.***, umbilical cord.

The diagram actually represents the fœtal circulation in ruminants; to make it applicable to the horse the ductus arteriosus (*d.v.*) must be supposed to be removed; the whole of the blood then traverses the liver by the union of the umbilical vein (*u.v.*) with the portal vein (*pt.v.*). The arrows indicate the course taken by the blood. Observe that the stream entering the right auricle divides, part passing into the right ventricle, and part into the left auricle through the foramen ovale (*f.o.*).

they are not yet prepared to receive the blood as they will be after birth, when they become distended with air, and have taken on their duties as breathing organs. The blood must therefore take another course than through the lungs. This course is provided by the *ductus arteriosus* (Fig. 253, *d.a.*), a short vessel uniting the pulmonary artery to the aorta, and thus bringing their lumina into communication. By this conduit the blood enters the posterior aorta, and is conveyed to the hinder parts of the body and to the placenta.

The allantoic or umbilical arteries convey the blood from the fœtus to the placenta. These arteries are branches of the internal pudics, or of the parent vessels, the internal iliacs, and during intra-uterine life they are larger than the parent vessels. Soon after birth, however, their walls become thickened, their lumina are lost, and they become impervious to the passage of blood. In the adult they are recognised as the thickened cords found in the lateral ligament of the bladder. The ductus arteriosus just prior to birth has a lumen easily receiving an ordinary cedar pencil, but it steadily diminishes until, at about a month after birth, it is no greater than the diameter of a knitting-needle. It is probable that little blood passes this way after birth, but the exact period of total occlusion is unknown. Similarly, the foramen ovale is blocked up by the development of a membrane, which may be pulled out with the forceps shortly after birth, and then resembles in shape an old-fashioned lace nightcap or cowl. When undisturbed, it lies in a heap, filling up the foramen.

The short cuts in the fœtal circulation—viz., the *ductus venosus*, *ductus arteriosus*, and *foramen ovale*—exist mainly with the object of ensuring that the purest blood reaches those organs which require it the most. The heart, head, and fore-limbs receive blood which is much purer than the blood circulating through the hind-limbs and abdominal viscera, for the brain must be well fed. The fact is that the fœtal blood at its best is far below the level of the arterial blood of the mother, and this is explained by saying that the demand of the fœtus for oxygen is small, owing to the low rate of its metabolism. From the blood of the umbilical artery and vein of the fœtal sheep the following gases have been extracted, and may be compared with the arterial blood of the mother :

	Umbilical Artery.	Umbilical Vein.	Maternal Arterial Blood.
Oxygen	2·3	6·3	20·0
Carbon dioxide.. ..	47·0	40·5	40·0

The liver is a very active organ in the fœtus, and is abundantly supplied with a mixture of blood, the worst and the best in the body, the best predominating. Early in intra-uterine life the liver begins to secrete bile, which is discharged into the intestines as meconium (see p. 234).

It is not known how the material passes from the maternal to the fœtal tissues; the blood of the two as previously mentioned, does not come in contact, but active changes occur between them through the villi of the placenta. Protein, fat, carbohydrate, and oxygen are received by the fœtus, and carbon dioxide, nitrogenous waste products, etc., delivered to the mother. The nourishment of the mother directly influences that of the embryo, and pregnant animals imperfectly fed can only produce puny offspring. The chemical changes between mother and fœtus in the human subject have been dealt with by P. Barr,* who shows from the nitrogen interchanges that the pregnant woman has a greater power of extracting from her food all the material required for the growth and development of the fœtus, and that at the end she has a balance to her credit. He considers, in the matter of nutrition, that a woman stands to gain, and not to lose, by pregnancy. That material may pass from mother to fœtus is proved by the bones of the embryo being stained if madder be administered to the parent. Yet it is known that the placenta, under other circumstances, is an efficient filter for certain pathological substances, and that the tuberculous mother does not convey tuberculosis to the fœtus. It has been suggested that the passage of water, salts, and sugar, from mother to fœtus may occur by diffusion, the passage of fat and protein being perhaps connected with special enzymes. The presence of glycogen in all the embryonic tissues points to it as an important material in the nutrition of the fœtus. Gradually, as development proceeds, the glycogenic function becomes largely centred in the liver and placenta.

Uterine Milk.—If the villi of the chorion be separated from the tubular depressions of the mucous membrane of the uterus, a fluid may be expressed, known as 'uterine milk.' This is particularly observable in separating the fœtal and maternal cotyledons. Uterine milk is of a white or rosy-white colour, creamy consistence, and contains proteins, fat, and a small proportion of ash. Examined microscopically, it is found to contain globules of fat, leucocytes, rod-like crystals, and structureless masses of protein. The use of the fluid is for the nourishment of the embryo, and in the mare, cow, and sheep the uterine glands take a prominent part in providing nourishment throughout fœtal life, pouring their secretion into special depressions in the placenta (Assheton).

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* *British Medical Journal,* October 28, 1911, p. 1118.

The **Duration of Pregnancy** appears to be based on no fixed law. Judging from the length of time the elephant is in gestation, it might appear that body size had an influence, but against this is the fact that the ass carries her young longer than the horse, while, whether it be a toy terrier or a Newfoundland, a dog goes from fifty-nine to sixty-three days. It certainly does appear that among animals of the same species breed has an influence in the matter; different herds of cows vary from 277 to 288 days, Merino sheep average 150 days, Southdowns 144 days. It is not clear why, of two rodents, the guinea-pig should require a period of gestation twice as long as the rabbit.

The following are average periods of gestation:

Elephant	2 years (nearly).
Mare*	11 months, and liable to vary within relatively wide limits.
Ass†	358 to 385 days.
Zebra	13 months (and over).
Cow ‡	40 weeks.
Sheep	21 weeks (average).
Camel	45 weeks.
Pig	16 weeks.
Dog	59 to 63 days.
Cat	56 days.
Rabbit	32 days.
Guinea-pig	63 days.

Parturition.—The fœtus having reached its full stage of development, changes of an obscure nature take place which lead to its expulsion. During uterine life the equine fœtus is lying on its back on the floor of the mother's abdomen, with its chin on its chest, the fore-legs bent at the knee, and the hind-legs in the right horn (Fig. 254). Preparatory to birth the fœtus changes position and turns on its side, so as to assume, first a lateral position (Fig. 255), and lastly an upright one (Fig. 256), by which the fœtal and maternal spines are brought nearer together. To assume this position the fœtus has had to make a complete revolution; it is now brought with the muzzle and fore-legs in the direction of the pelvis (Fig. 256), and dilatation of the passage follows. In the cow the fœtus lies on its back on the floor of the abdomen as in the mare, but somewhat crooked—viz., the head inclining towards one side, and the hind extremities towards the other; in all other respects it resembles the mare. The alteration in the position of the fœtus does not occur through its own movements, but by the contraction of the uterus; on the other hand, the stretching of the limbs is the result of fœtal movement.* There can be little doubt that the revolution of the fœtus prior to birth is the explanation of the complete torsion of the neck of the uterus and vagina which is sometimes found in both the cow and mare.

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* Tessier, in a memoir on the period of gestation presented in 1825 to the Royal Academy of Science in Paris, stated that in 582 mares, after one sexual congress, the shortest period of gestation was 287 days, the longest 419 days, a difference of 132 days. In 312 mares which visited the horse several times, the shortest period of gestation, calculated from the last cover, was 290 days, the longest 377 days, a difference of 87 days.

† Tessier gives the period of two asses, one being 12 months 20 days, the other 13 months 1 day; and these agree very closely with Sutherland's observations (*Veterinary Record*, October 13, 1894), quoted in the text above.

‡ Of 1,131 cows, the average period observed by Tessier was 240 days; the longest was 321 days (*Veterinarian*, vol. i., 1828).

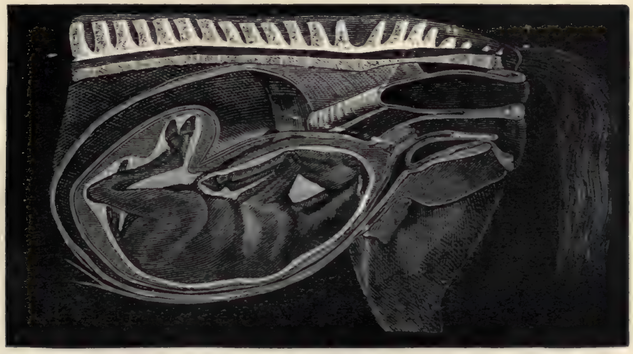

Fig. 254.—The Position occupied by the Equine Fœtus during Intra-Uterine Life (Franck).

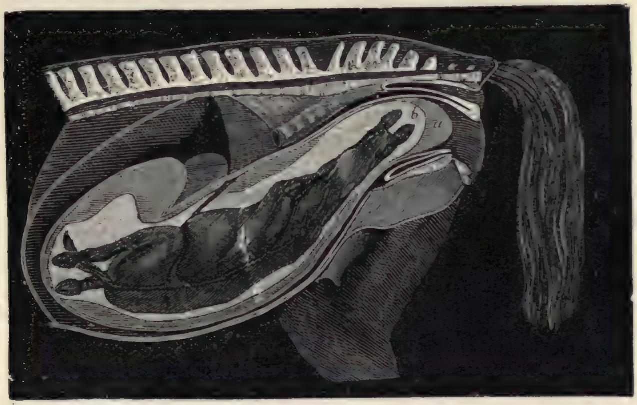

Fig. 255.—The First Stage in the Revolution of the Fœtus; Lateral Position. The Os is dilated by the Membranes which have not yet ruptured (Franck).

a, The Allantois; *b*, the Amnion.

The dilatation of the os is assisted by the amniotic and allantoic fluids. Each contraction of the uterus is accompanied by a pain; the pains last from fifteen to ninety seconds, and the interval between them is from two to four minutes. The contractions of the uterus occur under the influence of a centre in the lumbar portion of the cord; they are not under the control of the will, and occur even though the animal be unconscious, or the spinal cord divided in the lower cervical region (dog).

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* This description of the change in the position of the fœtus preparatory to birth is taken from Ellenberger's 'Physiologie' (after Franck).

The mare is remarkable for the rapidity with which delivery is effected; ruminants, on the other hand, are often very slow and in labour for hours. Parturition in the mare is accompanied by a complete separation of the chorion from the uterine wall; this is the explanation why any difficulty in delivery invariably sacrifices the life of the foal. In ruminants, on the contrary, the circulation between the mother and fœtus is to the last kept up by the gradual separation of the cotyledons, so that, though the process may be delayed several hours, the animal is generally born alive. The cause of the first respiration of the fœtus is dealt with at p. 138. Twin births are rare in the mare (in the thoroughbred approximately eight per thousand), and few survive; in the cow they are common.

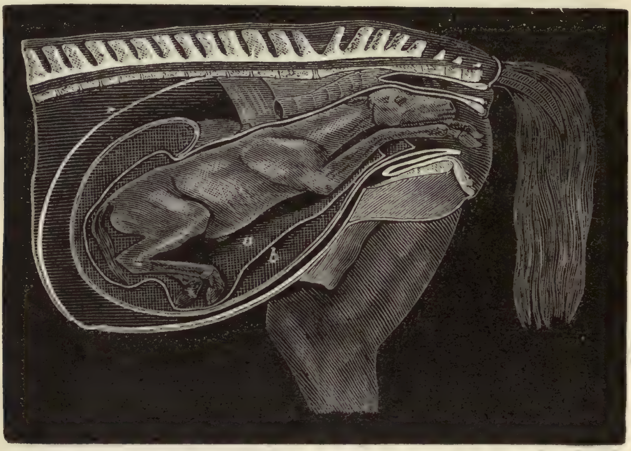

FIG. 256.—THE REVOLUTION COMPLETED, MEMBRANES RUPTURED, AND FOAL IN THE NORMAL POSITION FOR DELIVERY (FRANCK).

a, The Allantois; *b*, the Amnion.

SECTION 2.

The Secretion of Milk.

As the period of parturition approaches, the mammary glands become swollen, owing to active changes occurring in them, and at, or shortly after, the birth of the animal milk is formed. The nature of the sympathy existing between the generative apparatus and the mammary glands was, until recent years, quite unknown. The experiments of Lane-Claypon and Starling* have, however, indicated that the body of the fœtus contains a specific chemical substance (hormone), which, after absorption into the maternal blood, stimulates the growth of the mammary gland. This substance does not produce a secretion of milk; on the other hand, it inhibits it, and it is not until the womb is empty—*i.e.*, until after the birth of the animal—that, in consequence of no further hormones being produced, the secretion of milk begins. Other observers locate the seat of the hormone responsible for the growth of the mammary glands in the corpus luteum of the ovary, which, it will be remembered, grows to a considerable size during the first part of pregnancy. The essential features, however, are that a chemical substance is responsible for the growth of the mammary glands during pregnancy, and the withdrawal of this chemical substance from the body at parturition is followed by a secretion of milk.

Some evidence has been brought forward to show that the mammary gland is under the control of the nervous system, but the severance of all nervous connections does not stop secretion. The gland has even been transplanted in the guinea-pig to the neighbourhood of the ear, and functioned at the next parturition. Nevertheless, in the absence of a nervous connection it is difficult to explain the contractions which occur in a recently emptied uterus during suckling. The normal growth of the gland, apart from pregnancy, is regulated by the ovaries. These produce a substance which is carried by the blood, and leads to mammary growth. When the ovaries are removed, the glands atrophy. If the ovaries be removed from the cow when in full milk, lactation is maintained for a considerable period—it is said for as long as two or three years.

The stimulus to milk secretion, when once established, is suckling. In the absence of this, the glands after a day or two gradually lose their function, and the secretion ceases. A cow can withhold her milk by contraction of the muscular fibres of the teat duct. If her calf has been brought up with her, she may refuse to yield any milk unless the calf is present (see also p. 565). No animal, however, has the power of voluntarily discharging the gland when distended, and after this has reached a certain point the tension produces considerable pain.

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* *Proceedings of the Royal Society*, B, vol. lxxvii., 1906.

There are some unexplained phenomena connected with milk production. A dog, for instance, may, in consequence of copulation having occurred at the last œstrum, make her bed and produce milk, though pregnancy has never occurred. Such cases, though rare are beyond doubt. A mule may suckle a foal. This is even more difficult of explanation.*

Two processes contribute to the formation of milk. In one the cells lining the alveoli of the gland are shed bodily, and form the fat of the milk, while in the other the water, proteins, salts, etc., are formed from the lymph in the gland by the ordinary process of secretion. The first process must be examined at somewhat greater length. If the mammary gland of an animal which has never been pregnant be examined, the alveoli it contains are much smaller and less numerous than those of a secreting gland. The alveoli of the first-mentioned gland are found to be packed with small rounded cells of very slow growth ; when the animal becomes pregnant the gland enlarges, the alveoli increase in number, but remain packed with cells until parturition approaches or occurs. The solid masses of cells are now cast off, and leave behind them alveoli lined with a single layer of secretory epithelium, the function of which is to furnish the milk. The shedding of the mass of cells which originally occupied the alveoli supplies the colostrum or first milk.

The appearance presented by the single layer of cells lining the alvelous of the secretory gland depends upon whether the gland is loaded or discharged. If the gland is loaded—viz., active secretion occurring—the cells are found to be large and columnar in shape, possessing two or more nuclei, one being at the base of the cell, and the other, giving indications of degeneration, placed near the apex (Fig. 257). In the apex or free portions of the cell fat globules can be seen, which may even have partly extruded themselves from the cell, and besides these there are other particles. Further, the cell gives the appearance of the apex or free border being separated from the base by a process of constriction. If the gland be examined when discharged—viz., after the milk has been drawn off—the cells lining the alveolus are cubical or flattened, each containing a nucleus; the lumen of the alveolus is also increased in size, and within it may be seen some of the elements of the milk (Fig. 257). It is evident that the cells in the active gland are loaded with material, much of it being fat, and these cells break off, leaving behind them the parent cell, containing a nucleus from which another cell grows. In spite of this, the formation of fat in milk is really a process of cell secretion, and this is supported by the fact that animals such as carnivora, whose food is deficient in fat, produce a fat-containing milk, the fat being elaborated by the mammary cell from the protein of the body. A fat diet does not increase the fat in milk, though a protein diet has this effect.

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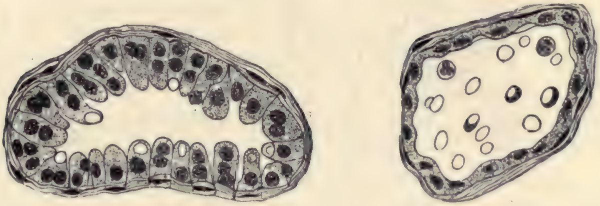
* The only case within the writer's knowledge occurred during the war in South Africa. The mule and foal were found on the veldt ; the general assumption was that the mule was the dam. This is out of the question ; the foal on the death of its mother no doubt attached itself to the mule, but the mechanism by which the mule produced milk in consequence of the foal sucking the mammary glands is unknown.

The proteins, sugar, and salts, found in milk are secreted in the ordinary way from the blood, or rather the lymph, circulating in the gland, the cells lining the alveolus being the active factor in the matter. That these substances are really elaborated by the cell is supported by the fact that neither caseinogen nor milk sugar exists in any other tissue of the body. It has been supposed that the secretion of milk is influenced by the nervous system, but there is no experimental evidence which places this beyond doubt.



Loaded. Discharged.

FIG. 257.—MAMMARY GLAND OF DOG DURING LACTATION. AFTER HEIDENHAIN (WALLER).

Composition.—The milk of herbivora has an alkaline reaction which may readily turn acid. In carnivora the reaction is acid. Fresh cow's milk is *amphoteric*—viz., it gives both an acid and an alkaline reaction to test-paper. This is due to the presence of acid and alkaline salts. In the cow the specific gravity is 1028 to 1034. The secretion contains proteins (caseinogen and albumin), sugar (lactose), fats, and salts. An average secretion of milk from a cow may be taken at 6 quarts (6·8 litres) per diem for forty weeks in the year. Assuming this to contain about 3 pounds (1·4 kilogrammes) of solids, it represents a production of solid matter during the milking year equal to that of the animal's body weight. The daily loss of material during lactation is made up as follows :

Protein	0·85 pound	(0·40 kilogramme).
Fat	1·25 pounds	(0·56 ,,
Lactose	0·85 pound	(0·40 ,,
Salts	0·12 ,,	(0·05 ,,

It is evident that a generous diet is necessary, not only in order to meet this loss, but to provide the needful energy for the great metabolic activity occurring during secretion, and to nourish the fœtus.

In the following table an analysis is given of the milk of different animals :

	Cow.	Mare.	Sheep.	Ass.	Dog.
Water	84·28	92·5	82-84	90·5	76·0
Solids	15·72	7·5	15-17	9·5	24·0
Casein	3·57	1·3	4·7	1·7	10·0
Albumin	0·75	0·3			
Fat	6·47	0·6	4-8	1·4	10·0
Lactose	4·34	4·7	3-4·6	6·4	3·5
Salts	0·63	0·3	0·6		0·5

It will be observed that the milk of the cow, sheep, and dog, is remarkable for the high percentage of fat it contains. The caseinogen of mare's milk is much less than that found in the cow, and more like that of the human. The milk of the dog is rich in caseinogen, fat, and calcium, but poor in lactose.

Proteins.—Under the influence of rennin, caseinogen becomes insoluble, and the milk is coagulated, resulting in a *clot* and *whey*. The clot or insoluble casein is now termed *tyrein*. Neither the albumin nor the caseinogen in milk is precipitated by boiling ; on the other hand, colostrum is precipitated by heating, and this is due to the fact that it contains globulin. The albumin of milk offers some peculiarities as compared with ordinary serum-albumin, and has been termed *lactalbumin*.

The **Fats** in milk are olein, stearin, and palmitin, and the proportion of these differs in various animals. The fat is contained within fat globules, and these form in milk a true emulsion, each globule being separated by a layer of milk plasma. On standing, the globules rise to the surface of the fluid and form cream. By the process of churning, the emulsion is destroyed, and the fat is obtained as butter. Butter consists of 68 per cent. of palmitin and stearin, 30 per cent. of olein, and 2 per cent. of specific butter fats.

Milk Sugar or *lactose* is very liable to undergo fermentation, resulting in the production of lactic acid and the curdling of milk. It is not, however, capable of undergoing direct alcoholic fermentation, which would appear to be a provision against fermentative decomposition occurring either in the gland or in the alimentary canal (Lea). The milk of the mare and cow in the presence of suitable ferments may undergo alcoholic fermentation, as in the production of *koumiss* and *kephir*.

The **Salts** of milk are principally calcium phosphate, and salts of sodium and potassium. In the composition of the milk an insight is obtained into the nature and quantity of the salts required by growing animals. Bunge gives the following ash analysis of mare's and cow's milk :

	Mare's Milk.	Cow's Milk.
Potassium	1·04	1·76
Sodium	0·14	1·11
Calcium	1·23	1·59
Magnesium	0·12	0·21
Iron	0·015	0·003
Phosphoric acid ..	1·31	1·97
Chlorine	0·31	1·69
Total ash per 1,000 ..	4·17	7·97

The phosphates are employed mainly in the construction of the skeleton. The excess of potassium over sodium salts is a feature common to many of the secretions of the herbivora, but probably in all animals the ash of milk contains more potassium than sodium. Bunge states that this is due to the fact that as the animal grows it becomes richer in potassium and poorer in sodium salts, depending upon the relative increase in the muscular structure, which is rich in potassium, and the relative decrease in the cartilaginous material, which is rich in sodium. Bunge compared the ash of a puppy with the milk of the mother, and the milk with the blood. It was remarkable how closely the composition of the puppy's system agreed with the salts it was receiving in the milk, though when the ash of the milk was compared with the ash of the blood of the mother, the greatest diversity in composition was apparent. In comparing Bunge's analysis of the ash of cow's and mare's milk, one is struck by the fact that the calf requires much more salts for its nutrition than the foal.

The first milk secreted is termed **Colostrum.** The source of colostrum, and some peculiarities in its composition, have already been dealt with. In appearance it is a yellowish-white fluid of an alkaline reaction, sweetish taste, and remarkable for the amount of protein it contains—as much as 15 per cent., whilst ordinary milk only contains 4 per cent. or 5 per cent. Examined microscopically, colostrum is found to contain bodies termed 'colostrum corpuscles.' These are large granular corpuscles containing fat. The use of colostrum is to act as a natural purge, by which means the intestinal canal of the newly-born animal is cleared out.

SECTION 3.

Heredity.

As no living thing arises spontaneously, but is built up from a pair of other living things (with certain exceptions in the lower creation) of the same species, it is probable that so long as man has been able to reason he has regarded the offspring of a given union as consisting of a mixture of its parents. As knowledge became extended, more especially since the origin of species has been traced almost step by step from the lowest to the highest, and shown to result from a common primitive form, the facts underlying these extraordinary changes have been the subject of inquiry, in order to determine the natural laws by which they are brought about.

The **Darwinian Theory** of the origin of species was based on the struggle for existence which arises wherever the capacity for reproduction is greatly in excess of the available food-supply. In the acute struggle the fittest must necessarily survive ; consequently this is determined by heredity. The transmission of favourable variations from parent to offspring must also in the subsequent stress afford those so endowed with greater powers of resistance, and consequently with a better chance of survival. The struggle for existence works in conjunction with natural selection. Darwin laid great stress on the gradual accumulation of small differences in the process of evolution, and he did not believe it possible for Nature to make 'jumps.' Extended experiments have shown that 'jumps' are occasionally made, and, moreover, such 'jumps' are heritable. The transmission of acquired characters was regarded by Darwin as a factor in evolution. We shall see presently that the consensus of present-day opinion is against the transmission of acquired characters, though those which are innate, and therefore born with the individual, are of course transmissible.

What has been stated of the impregnation of the ovum (p. 703) is sufficient evidence that both parents contribute in an equal degree to the construction of the offspring, and there is not much difficulty in the imagination conceiving that not only are the parents concerned, but their ancestors are represented, though in an ever-diminishing degree. An animal or a plant is therefore a mixture of its ancestors, but whether in this complex the individual characteristics remain distinct, or whether they are blended, is the question which at the present day is receiving the closest attention. If they are blended, fresh characteristics may in consequence arise ; if they are not blended, nothing can arise which was not conveyed to the new individual through the generative cells of its parents.

Galtonism.—That an animal is a mixture of its parents and their progenitors represents a bare statement of the law of heredity with which the name of Galton will ever be associated. As the result of his careful inquiries and elaborate statistical work on man and animals, Galton formulated a law known as *the law of ancestral inheritance*, which he stated as follows : 'The two parents between them contribute *on the average* one-half of each inherited quality, each of them contributing one quarter. The four grandparents contribute between them one quarter, or each of them one-sixteenth, and so on, the sum of the series, $\frac{1}{2}+\frac{1}{4}+\frac{1}{8}+\frac{1}{16}+$, being equal to 1, as it should be. The bias towards particular diseases, or tendencies to such diseases, by any particular ancestors in any given pedigree are eliminated by a law which deals only with average contributions, and the various prepotencies of sex in respect to different qualities, such as the familiar sex-limited diseases of pseudo-hypertrophic muscular paralysis, hæmophilia, and colour-blindness, are also presumably eliminated.' The essential feature to be borne in mind in connection with Galton's law is that it applies to masses rather than to the individual. It is an average result, the immediate parents in all cases being more largely represented than any of the other progenitors. For the improvement of a breed it is essential, according to Galtonism, that the laws of artificial selection should prevail, which, acting over a sufficient length of time, would blend in desirable proportions the special qualities required in the mass, though they might be absent in the individual.

Weismann's **Germ-Plasm Theory** of heredity broke away from the Darwinian view of the transmission of modifications from parent to offspring. He held that the use or disuse of any part, which under the Lamarckian doctrine would be transmitted to the next generation, is not so transmitted. In other words, there was no proof of acquired or somatic characters being heritable, and that the cases which had been brought forward to support this view could reasonably be explained by selection. Selection, he urged, was the prime factor in producing racial change, while environment had little, if any, influence. The germ plasm, he pointed out, was continued from generation to generation, but is subject to inborn transformation, and the environment selects the fittest or most suitable plasm through its finished product, the soma, the modifications so selected being transmitted to the next generation.

The **Mutation Theory** of de Vries was in sharp contrast to the fundamental principle of Darwinism, which laid down that changes were extremely slow and gradual. De Vries showed that in the case of certain plants variation arose suddenly. In consequence of this discovery the view that evolution was the result of minute differences acting through long periods was no longer regarded as necessary. Bateson had previously shown that the difference between species was not a gradual but a sharp one, and that intermediates did not exist. The continuity of the germ-plasm, on which Weismann took his stand, was thus not only called into question, but its exact opposite—*i.e.*, its discontinuity—demonstrated.

Mendelism.—The latest view of heredity is that put forward by Mendel many years ago, though it remained unrecognised until recently. It is difficult to define it in precise terms until examined, but it aims at applying physiological laws of inheritance to the individual rather than to the mass. It does not at present, and may never be able to, deal with all the characteristics of individuals. In the case of animals the application of Mendelian principles is as yet somewhat limited. Mendelian inheritance is known to exist in the matter of coat colour and length of fur in rabbits, and of the fleece in sheep. It applies to the coat of various breeds of dogs—*e.g.*, basset hounds and terriers. It also applies to eye colour. In the case of cattle and sheep it applies to coat colour and horns, and in dairy stock, it is said, to the quantity and quality of milk.[*] In poultry, to

[*] Professor J. Wilson, M.A., *Proceedings of the Royal Dublin Society*, 1910-11.

plumage, combs, feathered or clean legs, and extra toes, as opposed to the normal condition. In the horse it applies to coat colour, and, as Robertson* has shown, to 'staying' power, to the number of lumbar vertebræ, to the shape of the nasal bones, and shape of the ears in the race-horse, and in Shetland ponies to hock callosities. The principles apply much further in the case of plants, dealing with such features as height, characters of flowering-head, leaves, and stem, and have already been turned to useful economic account in husbandry by the production of new and improved species. The characters spoken of above are described in Mendelian phraseology as **Unit Characters.**

The union of the ovum and sperm-cell and their subsequent division, described at p. 703, enables the essential facts of Mendelism to be visualised. In Mendelian terminology either generative cell is spoken of as a **Gamete,** and the organism resulting from the union of two gametes is called a **Zygote.** We have seen that each gamete contains half the number of chromosomes found in the body cells, so that when the zygote is formed it is a double structure consisting of an equal contribution of chromosomes from each parental gamete. The resulting plant or animal retains in its cells throughout life the double structure imparted by the gametes. As was stated on p. 702, the inheritance of character is believed to be connected with the chromosomes.

We have seen that the cells in the living organism are divided into two groups—body or *somatic*, and reproductive or *germ cells* (p. 698). The absence of blending referred to on p. 731 refers solely to the generative cells. The soma, or body, is the envelope containing the generative cells, and between one generation and another there is no continuity in the cells of the soma. The link between generations lies in the germ cells. It is generally conceded that environmental conditions may modify the somatic cells of the individual, but that they exert no appreciable influence on the generative cells. Modification of the somatic cells not being heritable, it is to the influence of natural selection transmitted through the generative cells that variations must be attributed.

When a pair of zygotes breeds true for any given unit character, their gametes must in respect of that character be identical, and the resulting offspring of their union carries in its generative cells the same unit character. When two zygotes are mated which breed true for *opposite* unit characters, such as tallness and shortness in the common pea, the gametes produced by each, for the particular unit character of height, are not identical, but opposite. The resulting offspring in the *first* generation are not, however, in the matter of height, a mixture of the two zygotes; they take after one parent or the other, not after both, and whichever characteristic they follow is the **dominant** one; that which the body cells have not followed is the **recessive.**

But though the body, or somatic, cells of the offspring have followed the characteristic of either one or the other parent, their generative cells are a mixture of the unit characters of both. In spite of being mixed, there is no blending; the cells producing tall do not fuse with cells producing short plants, and subsequently result in those of medium size. The **determinant** or **factor** which produces tallness and the determinant or factor producing shortness, though both present in the generative cells of the zygote, are as clearly and sharply separated as if only one factor were present.

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* See footnote, p. 736.

When subsequently this zygote produces a generation, it will be found that half its gametes carry the factor for tallness and half carry that for shortness. This unblending or separation of the cells is described as **Segregation.** A single gamete must, in this way, be pure for either one or the other of two opposite characteristics ; in the example selected it must be pure for tallness or pure for shortness, inasmuch as we have seen that no blend of the two is possible.

The whole Mendelian structure pivots on the segregation of characters as outlined above, and the purity of the cells forming the gamete.

Had it been possible, we would have preferred to illustrate the theory of Mendelism by reference to experiments on animals, but Mendel's work was done on the common pea, and the essential facts are known in this plant with the greatest precision.

Selecting shortness and tallness from among several pairs of contrasting characters which the pea furnishes, Mendel found, on crossing a pure tall with a pure dwarf, that the offspring, or first generation, were all tall. This settled that in the pea tallness is *dominant* and shortness *recessive.* If the first generation be self-fertilised, a second generation is obtained. These are no longer all tall ; there are some short, and the proportion of tall to short plants is as three to one. The dwarfs of this generation, if bred among themselves, never produce anything but dwarfs, and so on in every succeeding generation. The dwarfs, we have seen, are recessive, and in Mendelian phraseology recessives breed true. The three talls of the second generation, if bred among themselves, behave as follows : One will produce all tall plants, and continue to do so to infinity ; the remaining two talls behave differently. They do not breed true, but each produces in a next generation talls and dwarfs, in the proportion of three talls to one dwarf. Of these, one tall and one dwarf breed true, while two talls are impure. These facts are shown in the following table :

Tall × Dwarf (Parents = P)

All tall (First filial generation = F1)

Tall, pure for ever	Tall, impure	Tall, impure	Dwarf (= F2), pure for ever

Reviewing the above classical example, it will be seen that the first generation, though all tall, contained in their generative, as apart from the body cells, the factors both for tallness and shortness. There was nothing in the appearance of these tall plants to indicate that they had a recessive character segregated, but it became evident in the second generation that three different plants existed—*e.g.*, a true tall, a true short, and an impure tall. In the third generation it was shown that the pure tall and pure short bred true, and that the impure tall bred pure talls and dwarfs and impure talls, in the proportion of three talls or dominants to one short or recessive.

The above example is the simplest form of Mendelian inheritance, and Mendel showed that each of the seven pairs of contrasting characters found in the common pea all behaved in the same way—

viz., for each of the distinguishing characteristics the dominant was to the recessive as three to one in the second filial generation, F2.

Dominance has been illustrated by Mendel's experiments on peas, in which it has been seen that the resulting zygote is a pure dominant when both gametes are pure for the particular character, and impure when only one gamete imparts the dominant variety. There is no difference in appearance between the pure and impure dominant above mentioned, but the test of breeding from them at once settles the question. In some cases a zygote differs from either parent by being intermediate in size or physiological properties, but their offspring follow the ordinary Mendelian law—viz., they reproduce the parental and the intermediate characteristics in the second generation. The parental characteristics in the next generation breed true; the intermediates behave as in the first generation—in fact, in accordance with the classical illustration of the peas. In such cases dominance is absent, and it is usual to state the fact by saying that dominance is not a necessary feature of Mendelian inheritance.

The following are examples of dominance in animals:

Bay dominant to chestnut in horses.
Grey dominant to black in rabbits and mice.
Black dominant to white plumage in fowls.
Polled dominant to horns in cattle.
Short coat dominant to long coat in rabbits, sheep, and dogs.
Feathered legs dominant to clean legs in poultry.
Extra toe dominant to normal condition in poultry.
Six lumbar vertebræ dominant to five lumbar in the horse.
Convex nasal bones dominant to concave in the horse.
Colour dominant to albinism in all animals.

No explanation can at present be offered why dominance is present in some cases, absent in others, and irregular in a third. In the following example of irregular dominance in sheep it is supposed that sex is the determining cause. Dorset horned and Suffolk hornless sheep were crossed, and the first generation resulted in the rams being horned and the ewes hornless. Bred among themselves, the several generations produced rams of which only three-fourths were horned, and ewes of which one-quarter bore horns. In this case horns or their absence depended upon sex, horns being dominant in the ram and recessive in the ewe. This was proved by mating a hornless ram with the hornless ewes of the first generation, the resulting progeny showing that half the rams were hornless and all the ewes.

Only an outline of Mendelism has been sketched above, and nothing but its simpler side explained. When applied to many cases of inheritance, Mendelism is not found to behave with the simplicity above indicated. For instance, it is no longer considered necessary to assume the existence of two factors to represent contrasting characters. Tallness or shortness in the pea is not due to a factor for tallness and another for shortness, but to one factor in two possible conditions—*e.g.*, *present* or *absent*. If present, the pea is tall; if absent, it is short. Two or more distinct factors in the gamete may also act on each other, and so influence the resulting zygote. This is known as the *interaction of factors*, and is a question of supreme importance to the Mendelist. Factors may also repel or attract one another; this is the theory designated the *repulsion and coupling of factors*. These are mentioned in order to illustrate some of the difficulties and complexities of the new doctrine; their consideration is beyond the scope of this work, and they require expert handling.

Evolution.—It is natural that Mendelism should be searched for an explanation of the evolution of the domestic from the original wild species. It is suggested by those to whose opinion great weight is attached* that the addition of factors, the subtraction, or the interpolation of factors will explain the little which is clearly known of evolution. For instance, there appears to be no doubt that the present sweet-pea in its many varieties arose from the wild sweet-pea introduced into this country a little more than two hundred years ago.† In this case the numerous present-day varieties have arisen, as is supposed, by the subtraction of factors. All the necessary elements for the production of the many civilised varieties are believed to have existed in the wild plant, but one by one those inimical to their production have been eliminated. The Mendelist does not reject the influence of variation, but he attaches to it a far stricter interpretation; he does not believe that variation need necessarily be small in amount, nor require ages to become adapted, for it can be shown that marked variations, known as 'sports,' may appear in a single generation. He further recognises two forms of variation: the one which may appear quite suddenly, and is transmissible by the gametes, since it is due to the existence of 'factors'; and the other which is acquired in consequence of the conditions of life under which the organism is living. The first has been called *mutation*, and has already been referred to; the second is *somatic fluctuation*, and, not being represented in the gametes, is consequently not transmissible. The process of evolution depends upon mutations, and natural selection determines whether their continued production shall be maintained or rejected. It is stated by Punnett‡ that a rare 'sport' with 5 per cent. selection in its favour will replace the normal in a few hundred generations. This being so, evolution generally demands a far shorter time for its production than has generally been supposed, and no better evidence in this respect can be brought forward than the improvement within recent generations of the breeds of domesticated animals, based on artificial selection.§

Mendelism is still in its infancy, and its application to the breeding of the larger stock, excluding poultry, has only been undertaken to the extent recorded at p. 735. There are difficulties in obtaining in animals the results readily effected in plants. One of these is that the sexes have to be provided by two distinct physiological units which may differ widely from each other, whereas in those plants, which are produced by self-fertilisation the constitution of the male and female elements is identical.

The laws of inheritance of such unit characters as coat and eye colour are known with considerable precision, but, as pointed out by Bruce,‖ the laws of inheritance of such unit characters as size, shape, fertility, vigour, endurance, are still unknown. These must be ascertained if exactitude is to replace the haphazard method of breeding at present in force. The whole trend of the work on heredity from the time of Darwin onwards has shown that it has a physiological basis, and this, in the hands of the breeder, even when employed in the dark, as hitherto, has yielded results of the highest economic importance. It is not too much to hope that the great precision given to heredity by Mendelism will in time replace the policy of 'hit or miss' by something approaching exactitude. Already it has explained, through the simple term 'recessive,' the previously incomprehensible fact that a character may 'skip a generation'; it also offers an explanation of *reversion* * and *atavism*.†

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* 'Mendelism,' R. C. Punnett, M.A., third edition, 1911.

† *Op. cit.* ‡ *Op. cit.*

§ In the matter of the race-horse, certain exact data are available for a considerable period, and the bearing of Mendelian inheritance on this animal has formed the subject of special study. See 'The Principles of Heredity applied to the Race-horse,' by J. B. Robertson, M.R.C.V.S., 1910. The writer takes this opportunity of acknowledging his indebtedness to Mr. Robertson's work, and his communications thereon.

‖ 'Mendelism and its Application to Stock-Breeding,' by A. B. Bruce, M.A., *Journal of the Board of Agriculture*, 1910.

Telegony is the supposed influence of a male by whom a female has previously conceived, on her subsequent offspring by another male. For generations this supposed influence was the dread of breeders. It possessed no physiological explanation, and was finally conclusively shown by Cossar Ewart to be without a shadow of foundation.

Heredity in Disease.—Of the influence of heredity in disease there is no possibility for doubt. Arrested development of the fingers in man, night-blindness, colour-blindness, hæmophilia, and a few other conditions, have been shown from constructed pedigrees to follow, or closely approximate to, the laws of Mendelian inheritance. So far as the hereditary diseases of animals are concerned, their Mendelian examination has barely begun, and in the very nature of things must take a long time to accomplish. Robertson has shown, from his inquiry into 'Roaring and Ruptured Bloodvessels in Race-horses,'‡ the possibilities awaiting patient investigations. On the question of the inheritance of disease considerable caution is necessary. There are few veterinary practitioners who, with experience of stock-breeding, are not impressed by the hereditary nature of such diseases as bone spavin, ring-bone, side-bone, 'shivering,' stringhalt, cataract, and navicular disease.

It may be that our ideas concerning the actual nature of the transmitted characters which lead to some, if not all, the above conditions will have to be modified. Chemical composition, or even molecular arrangement, may ultimately turn out to be the determining factor. No biologist would, for instance, assert that bone spavin was represented by a unit character, but he would accept the view that some particular condition of hock articular cartilage led to bone spavin. He would also admit that this specific cartilaginous condition might well be represented by a determining unit character, and that this character passed from parent to offspring. In these circumstances it is conceivable that bone spavin due to a defect or modification in the germ plasm would be heritable. On the other hand, if arising from sprain or trauma, its heredity would be absent, for somatic acquirements are not transmissible (Robertson).§

Robertson's investigations have shown that roaring, side-bone, 'shivering,' and a tendency to ruptured bloodvessel, follow the laws of Mendelian inheritance.

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* A return to some type of ancestral character, as when a black and a white rabbit produce a grey, which is the colour of the wild form. Chestnut is a reversionary character in the horse (Robertson).

† 'Throwing back,' or atavism, is the appearance of ancestral characteristics—as, for example, the extra digit sometimes found in the horse.

‡ *Op. cit.*

§ Communicated.

CHAPTER XIX

GROWTH, DECAY, AND DEATH

Growth.—The young of the herbivora very rapidly shake off the helpless condition in which they first find themselves in this world. This is largely due to the fact that they are born with a nervous system in a high state of development; in the course of a few hours they learn to stand and walk, and in a day or two can skip and run. The young animal, moreover, is born in full possession of its senses, such as sight, touch, hearing, smell, taste, and with an amount of intelligence which nearly, if not quite, equals that of its parents. It has practically nothing to learn but obedience to man. Not only is the nervous system in an advanced condition, but also the locomotor. The legs of the foal are remarkably long, some of the bones being nearly their full length, though, of course, not their full weight; such joints as the knee and hock have very little to grow. We can understand the reason of this development of the limb from what has been said above, while the length of leg in the foal is undoubtedly for the purpose of enabling the animal to reach the mammary gland. The limb, however, is only partially developed; from the knee and hock to the ground it is nearly the length of the adult; from the knee to the elbow and the hock to the stifle it is decidedly below the adult; whilst from the elbow to the withers, and the stifle to the croup, the body has a considerable amount to grow. It has been said, and the statement appears to be true, that the future height of the foal may be ascertained by measuring the fore-limb from the fetlock to the elbow and multiplying it by two.

The hind-quarters of the foal are in a more advanced state of development than the fore: the shoulders are very oblique, the chest contracted and shrunken-looking, and neither contains much muscle. The oblique position of the scapula is due to the weight of the body on the limbs, the weakness of the muscles at this part allowing the angle formed by the scapula and humerus to be considerably closed, and the shoulder-joint to bulge. The head of the foal is prominent over the brain and depressed over the nasal bones. The hair is fully developed but woolly, that of the mane being scanty and of the tail curly, while the colour of the body-hair is light of its kind. A similar deficiency of pigment is observed in the iris.

TABLE SHOWING THE LENGTH OF THE BONES OF THE LIMBS OF THE FOAL AND ADULT HORSE.

	Adult Horse.	Foal of Six Weeks.	Difference.
Scapula - - -	15 in.	8¼ in.	6¾ in.
Humerus - - -	12 in.	8 in.	4 in
Radius and ulna - -	18 in.	12 in.	6 in.
Knee-joint - - -	3½ × 3½ in.	3 × 3 in.	½ in.
Metacarpal - - -	9½ in.	8¾ in.	¾ in.
Suffraginis - - -	3½ in.	3 in.	½ in.
Femur - - -	17 in.	10½ in.	6½ in.
Tibia - - - -	13½ in.	9½ in.	4 in.
Calcis to metatarsal bone -	6 in.	5 in.	1 in.
Metatarsal - - -	11 in.	10 in.	1 in.
Suffraginis - - -	3½ in.	3 in.	½ in.

The rate at which the foal increases in weight, and other circumstances connected with its nutrition, were made the subject of inquiry by Boussingault.* He found that the mean weight at birth was 51 kilogrammes (112 pounds), that during the first three months the daily increase in weight was 1 kilogramme (2·2 pounds), from three up to six months the increase was 0·6 kilogramme (1·3 pounds), and from six months up to three years of age the increase was at the rate of 0·32 kilogramme (0·7 pound) per diem. The influence of feeding on development is most remarkable. Not only does the body increase in size and weight, but the animal presents the appearance of the adult, so that a thoroughbred at two years old is 'furnished' and looks as old as an ordinary horse at four years old. Calves, according to Torcy,* have a mean weight at birth of 35 kilogrammes (77 pounds), the daily increase during the first two years being 0·7 kilogramme (1·5 pounds). With sheep the daily increase in weight is more rapid. A lamb will in ten days gain 50 per cent. on its original weight, will double its weight at the end of the first month, and treble it at the end of the second. Swine present, however, the most rapid increase in weight, for, according to the authorities quoted, a pig will increase 20 per cent. in its weight per diem during the first week, and up to the end of the first year will add 0·2 kilogramme (0·44 pound) daily to its body weight.

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* Quoted by Colin.

The relative rate of growth of each part is not the same. The eyes, ears, brain, kidneys, and liver grow less rapidly than the other parts, owing to their relatively large size at birth. The greatest increase is in the skeleton and muscles, and to the rate of this increase we have just alluded; the least increase is in the eyes and the ears and the limbs below the knee and hock. Few observations have been made on the rate of growth. Percival* many years ago drew up a table, which he considered very imperfect, as to the rate at which some horses of his regiment grew, from which he showed that the increase in height between two years and three years was on an average 1 inch, between three years and four years ⅓ inch, and between four years and five years ⅓ inch. Some of the horses did not grow.

Of 35 two-year-olds, 2 did not grow during the year.
Of 144 three-year-olds, 17 did not grow during the year.
Of 48 four-year-olds, 7 did not grow during the year.
Of 11 five-year-olds, 2 did not grow during the year.

There can be no doubt that many horses grow much more than ⅔ inch between three and five years, and many grow up to their sixth year.

The writer measured the daily growth of a foal for three months, the observations being made at the withers and croup. The animal during this period grew, on an average, one inch every eight days. The most rapid growth occurred shortly after birth and was one inch in three days. Both at the withers and croup the rate of growth was practically equal.

During the time the calf and foal are receiving their mother's milk the urine is acid, for the reason that the animal is practically carnivorous. Once a vegetable diet is taken, the urine becomes alkaline and, it is probable, decreases in quantity. The activity of certain glands, such as the thymus, becomes considerably reduced as the animal grows, and finally disappears at the adult period. One characteristic of the young animal is the necessity for sleep. It is probably during slumber that the tissues make the immense strides noticeable during the first few weeks of life.

Dentition commences immediately at birth, if it has not already commenced *in utero*. The following tables show the period at which changes take place in the teeth from birth to adult age.

The periods of eruption and change of the molar teeth are liable to considerable variation.

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* 'Lectures on Form and Action.'

Horse.

	Eruption.	Change.
Incisors :		
Central - -	At birth.	2½ years.
Lateral - -	1 to 2 months.	3½ years.
Corner - -	7 to 8 months.	4½ years.
Molars :		
First - -	At birth.	2½ years.
Second - -		3 years.
Third - -		About 3½ years.
Fourth - -	About 1 year.	
Fifth - -	About 2¼ years.	
Sixth - -	About 3½ to 4 years.	
Canines - -	About 4½ years.	

Ox.*

	Eruption.	Change.
Incisors :		
Central - -	At or soon after birth.	$1\frac{9}{12}$ years.
Middle - -		$2\frac{2}{12}$ to $2\frac{6}{12}$ years.†
Lateral - -		$2\frac{6}{12}$ to 3 years.†
Corner - -		$2\frac{10}{12}$ to $3\frac{6}{12}$ years.†
Molars :		
First - -	At birth.	About $2\frac{3}{12}$ years.
Second - -		About $2\frac{3}{12}$ years.
Third - -		About $2\frac{6}{12}$ years.
Fourth - -	6 months.	
Fifth - -	About 12 months.	
Sixth - -	21 months.	

Sheep.

	Eruption.	Change.
Incisors :		
Central - -	At birth or soon after.	About 1 year.
Middle - -		About 2 years.
Lateral - -		Soon after 2 years.‡
Corner - -		About 3 years. ‡
Molars :		
First - -	At birth or soon after.	Soon after 18 months.
Second - -		
Third - -		About 2 years.
Fourth - -	3 months.	
Fifth - -	9 months.	
Sixth - -	18 months.	

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* The age of the ox, sheep, and pig is tabulated from the data given by Professor Brown in his 'Dentition as Indicative of the Age of Animals'; the observations were made by Professor Simmonds.

† There is considerable variation in the date of development of these teeth.

‡ These teeth are liable to great variation in their date of development.

PIG.

	Eruption.	Change.
Incisors :		
Central - -	1 month.	12 months.
Lateral - -	2 months.	18 months.
Corner - -	At birth.	8 months.
Molars :		
First - -	1 month.	About 15 months.
Second - -		
Third - -		
Fourth - -	5 months.	
Fifth - -	10 to 12 months.	
Sixth - -	18 months.	
Premolars - -	5 months.	
Tusks - -	At birth.	9 months.

In all these tables the periods given are those of eruption only. The teeth are not fully developed for some time later, which varies from four to six months in the horse to a month in the pig and ruminant. Culley* noted that the central and lateral temporary incisors attain their full growth in the foal fifteen days after appearing, but that the corner teeth take one and a half years to reach their full length. Without being committed to this period, it is certain the corner temporary teeth are much slower in coming into wear.

The completion of dentition usually marks the age of maturity. The uncastrated animal presents very distinctive features as compared with the female—viz., greater bulk, a heavy crest and neck, and a harsher voice ; the castrated horse more closely resembles the mare. No such difference in the date of maturity as is observable in the human family exists between the male and female of the horse tribe. The mare arrives at maturity at the same time as the horse, and the castrated animal is not deficient in stamina, strength, or capacity for work. Moreover, castration in the horse does not lead to a deposition of fat in the body.

Decay.—It is doubtful to what age a horse would live if not subjected to domestication, but we may safely say that at seventeen years old, which probably represents fourteen years' work, the powers of life in the majority of them are on the wane, though at this period some may be found in full possession of life and vigour. These are probably cases of a survival of the fittest, and cannot be taken as a general guide. As a broad rule it may be stated that an old horse is liable to be killed by a hard day's work, and in this sense he is certainly old at seventeen. A general arterial degeneration is not marked at this period of life, and few horses live long enough for their arteries to become rigid. The mean age at death of thoroughbred stallions is slightly under twenty years.

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* *Op. cit.*, p. 649.

Doubtless the work performed by horses is the chief cause of their rapid decay, for their legs always wear out before their bodies. But apart from this, changes in their teeth, such as the wearing away of the molars, appear to prevent many of them from reaching a ripe old age. Instances are on record of horses attaining the age of thirty-five, forty-five, fifty, and one animal is known to have lived to sixty-three years of age.* Blaine† appears to have gone very carefully into the question of old age in equines, and he drew the following comparison, which is doubtless very close to the truth: 'The first five years of a horse may be considered as equivalent to the first twenty years of a man. Thus, a horse of five years may be *comparatively* considered as old as a man of twenty; a horse of ten years as a man of forty; a horse of fifteen as a man of fifty; a horse of twenty as a man of sixty; of twenty-five as a man of seventy; of thirty as a man of eighty; and of thirty-five as a man of ninety.'

The duration of life in the various domesticated animals is given by Crisp‡ as follows:

Horse - -	25 to 35 years.	Goat - -	15 years.
Ass - -	30 to 40 years.	Sheep - -	15 years.
Ox - -	15 to 20 years.	Pig - -	12 to 16 years.
Dog - - -	14 years.		

It is believed these observations were made under the favourable conditions of animals in captivity (Zoological Gardens), well fed and looked after, and the figures are in consequence high. Bracy Clark § regarded the horse as not mature until the eighth year, and that this period multiplied by four would be somewhere about the natural duration of his life. He stated he had seen horses at thirty-two years of age capable of 'a great deal of service.'

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* Bracy Clark, in his 'Podophthora,' quoting from the *Liverpool Advertiser*, said there was a cart-horse on the canal near Warrington sixty-three years of age. Clark knew of a hunter fifty-two years of age that had never been out of the hands of the man who bred him.

In a morning paper of May 17, 1911, it is stated that a farmer in the Lake district owns a horse forty-three years of age which still occasionally works.

In an article entitled 'Is a Horse Old at Fifty?' published in the *Standard*, December 25, 1893, a number of interesting facts connected with the age of death of famous horses is extracted from the earlier volumes of the stud book.

Parrot died at 36.
Pocahontas died at 33.
Matchem died at 33.
Competitor died at 30 (the last of the Eclipses).
Touchstone died at 30.

In the above article there is no reference to Eclipse. He died in his twenty-sixth year.

The age at death of more modern thoroughbred horses is as follows: Hermit 29, Victor 29, Gunboat (by Sir Hercules), shot at 29; Voltigeur, destroyed for fracture at 27. Melton died 29, St. Simon 27, King Tom 27, Bend Or 26, Rosicrucian 26.

† 'Outlines of the Veterinary Art.'

‡ *Op. cit.*, p. 694.

§ 'Podophthora.'

Death.—Death from natural causes in the horse is a matter of rare occurrence. It is seldom that an animal is taken such care of that the tissues are worn out by age and decay, or that he is allowed to live until the breath of life passes gradually from the body. Sentiment plays no part in horse management. A useless mouth is one to be got rid of. In consequence, the majority of horses meet either with a violent death or one the result of disease. Under good hygienic conditions the general death-rate may be taken at 1·5 per cent. To this, however, must be added a fluctuating loss due to destructions for injury, which may be stated at about 1 per cent., depending on the occupation.

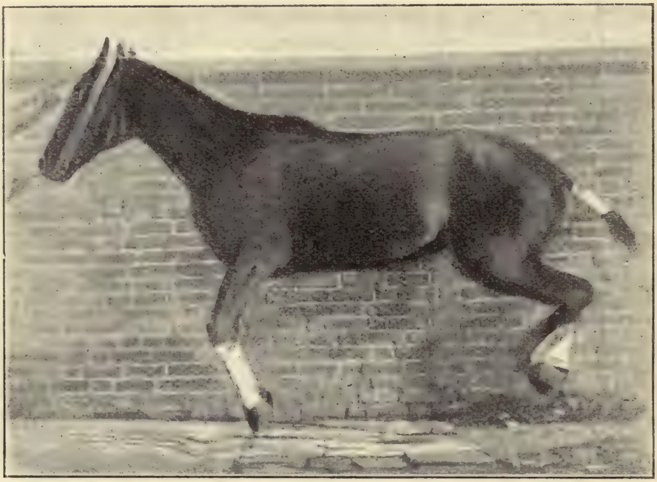

FIG. 258.—CONVULSIVE LIMB MOVEMENTS AT THE MOMENT OF BRAIN DESTRUCTION.

Note the tail is affected as well as the limbs. The bandages were put on to assist the plate.

Natural death is described as commencing either at the heart, lungs, brain, or blood. Probably the few cases of natural death which occur may be attributed to failure of the heart's action; but from what is known of the physiology of the heart, respiration, and blood, it is very difficult to separate these in discussing the causes of death, knowing how largely one is dependent on the other. The cessation of the heart's action may be looked upon as the termination of life.

We cannot enter upon the cause of death the result of disease, excepting to notice the interesting fact that horses seldom die quietly. A large majority of them leave this world in powerful convulsions, fighting or struggling to the last, lying on their side, and galloping themselves to death. Especially is this marked in acute abdominal trouble. The struggles at the end should not be mistaken for pain: the animal is quite unconscious. The violent convulsions which occur at the last moment are not present in death from acute chest diseases; such cases stand persistently to the last, and either drop dead or die very shortly afterwards.

In violent death by destruction of the brain in horses, remarkable muscular contractions of the limbs occur. These cannot be seen with the unaided eye, as they are so rapid, but are readily revealed by the camera (Fig. 258). In spite of their rapidity, a marked interval between brain destruction and muscular contractions occurs. In Fig. 259 the brain was destroyed by a charge of large shot, yet the horse is still standing, the impulses producing convulsive limb movements not yet having had time to pass out. At the moment of violent death the bladder and rectum are emptied, the penis protruded, the horse sweats on the inside of the thighs, the pupils dilate widely, and occasionally, when all seems at an end, the *panniculus* is called into play, and the animal may shake the skin with re-

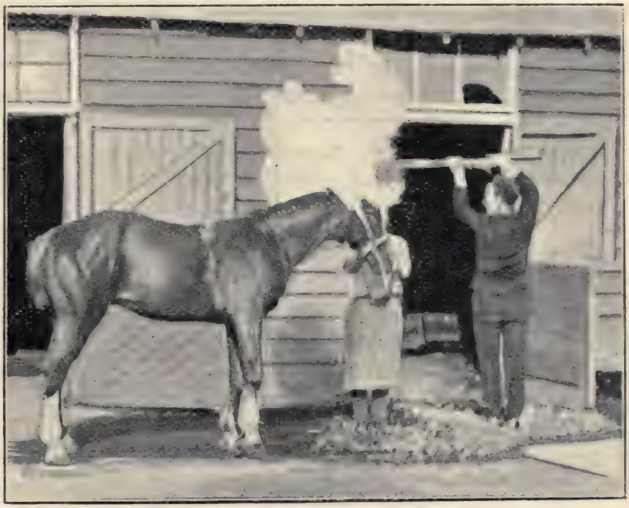

Fig. 259.—Brain destroyed by a Charge of Shot.

The head has slightly dropped; muscles of the quarters are preparing to contract, as may be seen by their outline; the tail is also turned to one side, and the heel of one limb has left the ground. There is nothing, however, to indicate the fact that the horse is dead.

markable vigour, as if to dislodge a fly. The heart may continue to beat for a minute or two, but the respirations cease. As life is being extinguished the *ligamentum nuchæ* exercises its elastic recoil in the absence of muscular resistance, and the head is drawn back momentarily with slight jerks until the muzzle projects.

Soon after death *rigor mortis* appears (see p. 418), and within a short time tympany of the abdomen is apparent in the herbivora, reaching such a degree in a few hours, especially during warm weather, that post-mortem ruptures of the diaphragm and other viscera are exceedingly common. The explanation of the tympany is the considerable amount of gas generated by the fermentative decomposition of vegetable food. With death-stiffening the flexor muscles of both fore and hind limbs contract in excess of the extensors, so that the heels of the feet are slightly drawn up; the ears are also drawn back.

The Influence of Age on Capacity for Work.—It has been pointed out (p. 97) that the horse, unlike man, does not fail in his heart and arteries in consequence of increasing age. It is not, therefore, a matter for surprise that up to a late period of life he does not lose his capacity for work. In this respect he offers a great contrast to man. At forty years of age there are few men capable of undergoing fast muscular work on their own limbs, for not only are the muscles slower in responding, but the effort required is greater. A child may, indeed, execute with ease muscular movements which would produce a punishing effect on a middle-aged man. If it be accepted that a horse of fifteen is comparable to a man fifty years of age, then it is certain no man of fifty can perform the relative amount of work which a horse can at the corresponding age. With increase in age, horses lose elasticity of tread, but not power for work, even relatively fast work. This applies both to the thoroughbred and other classes.

No explanation of the fact can at present be offered. It may, perhaps, yet be shown that the vertical position of man exercises a strain on the heart and vessels which is absent in the horizontally placed animal. Or there may be some actual defect in the skeletal muscles of man, the result of age, which is unknown in the horse. Trotting work soon wears a man out; the Japanese and Natal coolie, who pulls a light cart containing one or two people, only lasts three years. He then has to look for lighter employment. A horse performing relatively equivalent work would last much longer.

Horses of sixteen or seventeen years of age undoubtedly show a falling off, not only in pace, but especially in recuperative capacity after prolonged and severe exertion. This does not in any way detract from the general statement, and remarkable fact, that the horse works equally well at all ordinary periods of life, and in this sense does not grow old.

CHAPTER XX

THE CHEMICAL BASIS OF THE BODY*

A LARGE number of elements enter into the composition of the body—oxygen, hydrogen, carbon, nitrogen, sulphur, phosphorus, chlorine, iodine, fluorine, silicon, potassium, sodium, calcium, magnesium, and iron. Only to a very limited extent are these found free in the body. They are generally brought together in such a way as to form compounds, and these are divided into two main groups—organic and inorganic.

The organic group consists of protein, a little carbohydrate, and fat. The same substances are found in plants, though not in the same proportion. In the great cycle of events in the universe, nothing is lost—plants build, animals destroy. The products of destruction find their way back to the earth to be utilised by plants, and once more served up for the use of animals. Plant life is synthetic, and the chemical processes are mainly those of reduction ; animal life is analytic, and the chemical processes mainly those of oxidation. The plant converts kinetic into potential energy, while in animals the reverse process occurs, and the potential energy contained in food is converted into kinetic. A simple, though vast, cycle of reciprocal events is occurring between vegetable and animal life.

The common platform on which these meet is the cell, which has been briefly considered at p. 698. The structure, chemistry, and physics of the cell is the same everywhere. Widely as cells may differ in shape, they conform to a common structural and functional plan in plants and animals, the essential feature being the protoplasm for nutrition and the nucleus for reproduction. Of the highly complex protoplasm but little is known. It behaves as living material in that it requires food and oxygen ; it digests and excretes ; it moves, behaves as if it had sensation, reproduces itself, and finally becomes worn out and dies. Of the nucleus still less is known, while as to the causes which lead to its reproduction complete ignorance prevails. All the elements found in the body of the animal or plant are discovered in the protoplasm. Protein, fat, sugar, starch, and salts exist in this minute speck of life, and yet only form one-quarter of its weight, while the remaining three-fourths are water. Simple in structure as the cell is of which we have been speaking, there is great reason for believing that it does not represent the earliest form of living material. What the connection is, if any, between the most elementary form of living or dead material is at present unknown, but the division of chemistry into organic and inorganic is rapidly being broken down under the recent extraordinary advances into the structure of the atom made by modern physico-chemistry. There are some who look upon the mysterious ferments as the go-between. We shall glance at these remarkable bodies presently, of which so little is known, but which some believe hold the key to the solution of the problem of the origin of life.

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* It is not intended in this chapter to do more than to elucidate and supplement some of the chemical statements scattered throughout the previous chapters.

The organic substances of the body are sharply divided into two important groups—those containing nitrogen and those nitrogen free. To the nitrogenous class belongs the all-important and complex group of proteins ; to the non-nitrogenous class belongs the fat and the small amount of carbohydrate, such as sugar and animal starch, found in the body. The inorganic substances are represented by the elements and their salts, and it is convenient to deal with this group first.

The Inorganic Bodies.

The inorganic substances found in the body are water, gases, and salts. **Water** forms 60 per cent. of the whole body, the bulk of which is taken in with the food and water, only a small quantity being produced in the organism. The water supplied to the system furnishes no potential energy, and consequently no nutrition.

The **Gases** found are oxygen, nitrogen, hydrogen, carbon dioxide, sulphuretted hydrogen, and marsh gas. **Oxygen** is the most widely distributed of the elements, forming one quarter by weight of the atmosphere, and eight-ninths by weight of water. By means of its compounds it forms one-half by weight of the earth's crust. It is practically the only element which enters the animal or vegetable body in a free state, and in plants it does so only to a limited extent, for these obtain the bulk of their oxygen through the decomposition of carbon dioxide and water. In the animal body it exists free and combined in some of the body fluids, such as blood ; others, such as lymph, contain only traces, and none can be obtained from the most bulky tissue of the body — *i.e.*, muscle. Of the two great cavities of the body—the chest and abdomen—one is remarkable for containing the oxygen absorbing and distributing apparatus, the other contains the digestive canal, which carries out its work in the entire absence of oxygen. **Nitrogen** exists largely in a free state, since it forms no less than four-fifths of the atmosphere, while it has but little affinity for other elements. In the form of ammonia, nitrous and nitric acids, it enters the plant through its roots ; as protein it enters the animal, leaving it as urea, etc., which by decomposition readily yields ammonia. The animal cannot utilise free nitrogen any more than the plant can, though leguminous plants utilise atmospheric nitrogen by symbiotic co-operation with nitrifying bacteria. There are nitrifying and de-nitrifying bacteria. The former oxidise ammonia and nitrites into nitrates, and are capable of assimilating the free nitrogen of the atmosphere, which they fix and supply to the plant. The latter set nitrogen free by reducing nitrates to nitrites, and decomposing nitrites into nitrogen. From the nitrifying bacteria in plants protein can be built up out of inorganic salts in the absence of chlorophyll. **Carbon** is present in the atmosphere in small amounts united to oxygen—*i.e.*, in the form of carbon dioxide. It is only in this form that it can be taken up by plants, which in their special laboratory split off the oxygen molecule and store up the carbon, returning the oxygen to the air, and thus supply to the atmosphere that element of which animals are continually depriving it. Under the influence of the ultra-violet rays in light, the green leaves of plants are capable of manufacturing sugars and starches from carbon dioxide and water. Carbon enters the animal system with the carbon of the food, and leaves it either as carbon dioxide or in compounds, such as urea ; as carbon dioxide it is again taken up by the plant. There is no solid or fluid tissue of the body free from carbon dioxide. It is the most widely distributed gas in the body.

The **Salts** of the body are contained in every solid and fluid tissue, though not always in the same proportion. In bone it is naturally high. The age of the animal influences the amount of salts in the body, young growing animals storing up material which the adult rejects. The salts found are those of sodium, potassium, calcium, magnesium, and iron, in the form of chlorides, sulphates, phosphates, and carbonates. The nature of the diet influences the character of the salts present—for example, vegetable food is rich in salts of potassium and poor in those of sodium. The salts contribute no energy to the body, but their function in nutrition is of the utmost moment. They direct in some unknown way the metabolism of the body. A salt-free diet produces death from what has been termed **salt-hunger.** No matter how liberal the diet may be in organic matter, if the salts be removed from it death ensues : in the case of the dog in about six weeks or even less. It has been supposed that life could be preserved longer under starvation, provided ample water be supplied, than on an unlimited diet which is salt-free. This being the case, the extraordinary importance of saline matter in the food is evident. At present very little is known of the subject, but it is generally believed that when the full story is known, it will be found that each salt has a special function to perform in nutrition. Bunge is of opinion that the salts of calcium and iron which enter the body with the food are in organic combination, and that they could not be replaced by inorganic salts. The great test case is iron, which is largely prescribed clinically in an inorganic form. Yet this is attended with success, and an increase in iron can be demonstrated in the blood and tissues. Nevertheless, it would appear that salts in organic combination are more readily taken up than those not so combined.

An interesting question arises in connection with the artificial supply of **common salt** for animals. It is popularly believed that the herbivora have a craving for salt, and in a wild state proceed to certain 'salt-licks' periodically to obtain a supply. Bunge explains this by showing that vegetable food is particularly rich in potassium, and especially poor in sodium, and that the effect of potassium salts is to withdraw those of sodium from the system, through the potassium combining with the chlorine and being removed by the kidneys. He points out that man takes common salt as an addition to his diet, to meet the loss caused by eating vegetable food, but makes no attempt to supplement the supply of other salts ; further, that carnivora avoid salted food, as sufficient sodium chloride exists in flesh. Notwithstanding Bunge's authority, it is quite certain that horses may be kept in perfect health without any addition of sodium chloride to their food, and what applies to them probably applies to other herbivora.

Sodium salts in the blood are essential to its proper osmotic pressure, but both sodium and potassium are antagonistic to calcium by promoting relaxation instead of contraction of the heart wall. Speaking generally, the sodium salts are found in the fluids of the body, those of potassium in the solids, though it will not be forgotten that in this respect the sweat of the horse is an exception, being rich in potassium salts.

The remarkable part played by **calcium** in the matter of blood and milk clotting has already been referred to, also the influence of a saline solution in maintaining the rhythmical contraction of the heart. The oxygen-carrier of the body would not be an oxygen-carrier but for its iron, which renders the production of hæmoglobin possible. In the absence of salts the secretions would be useless, and those containing globulins would precipitate, as it is the salts which keep these in solution. In the case of young growing animals, the skeletal structure would fail through loss of calcium and phosphoric acid—in fact, there is no tissue of the body which would not be more or less affected by a shortage or entire absence of salts.

Bunge supposes the salts of calcium enter the body in an organic compound, but that those of sodium, potassium, and magnesium enter and leave the body as inorganic salts. Attention is now being directed to the calcium content of blood as a clinical factor, its excess or deficiency being believed to play an important part, particularly in disorders of the circulatory apparatus. It was Ringer who, years ago, urged the importance of calcium in connection with the circulation, and we have seen (p. 49), as the result of his work, that it is now known the mammalian heart may be kept beating for hours on removal from the body, if fed with Ringer's solution and liberally supplied with oxygen. The relative part which each of the salts of calcium, sodium, and potassium are believed to play in this phenomenon has already been noticed. Calcium is especially necessary to the contraction of the heart, which can be shown to cease beating on decalcifying the blood, and its contraction restored on adding calcium in proper proportion, for an excess has the opposite effect and stops the heart. Lime exists largely in clover and hay, but only in small quantities in the cereal grains. It is principally in the hay that the amount excreted by horses through the kidneys is supplied. In the urine it passes from the body in such quantities that it cannot be held in solution by the alkaline fluid, and the urine of the horse is therefore always turbid. In the body calcium exists in the form of phosphate, sulphate, and carbonate, in the urine principally as carbonate and some oxalate. The amount of lime in some of the secretions may be judged from the fact that in saliva it falls as a deposit on the fluid standing, and in cow's milk it represents a loss to the animal of 42·5 grammes CaO (1·5 ounces) every twenty-four hours.

Phosphorus enters plants as phosphoric acid united with alkalis. In soils it exists in only small quantities, hence the necessity of phosphates as manure. In the plant phosphoric acid forms a part of the complicated compounds known as lecithin and nuclein, in which condition it enters the animal body, forming a part of both the solid and fluid tissues. Once in the tissues, the body holds on firmly to its phosphates, and only parts with them under pressure.

A deficiency of organic phosphorus in the food appears to be connected with a form of polyneuritis. Animals* fed on rice, barley. or wheat flour, in which the outer layers of the grain have been removed by milling, contract a disease apparently identical with a form of beri-beri in man. This may be cured by the administration of organic phosphorus in the form of beans, peas, testicular extract, pancreas, or bran. The disease may even be prevented if these be added to the incriminated diet. It is not known whether the affection is due to the absence or deficiency of any special member of the group, such as lecithin, nuclein, etc. Hutcheon, in South Africa, showed the advantage of feeding on bone-meal in cases of *osteo-malacia* in cattle.

Phosphates are united with soda, potash, lime, and magnesia. The foods richest in phosphoric acid are oilcake and bran, while hay and straw are poorest in this substance. Phosphoric acid is principally excreted by herbivora with the fæces, only small quantities passing away with the urine.

Magnesium salts occur in the body principally as phosphates, and in this form they enter largely into certain foods, such as oats. The amount of magnesium passing away from horses through the kidneys is small, but considerable quantities derived from the food pass out with the fæces, as they cannot be utilised in the body. By collecting in the bowels, this salt produces the ammonio-magnesium phosphate calculi so common in horses.

Sulphur exists largely in nature in combination as sulphates of alkalis and alkaline earths. In this form it is taken up by plants, and, becoming a part of their protein molecule, finds its way into the body of the animal, where, by splitting up and oxidation, it yields sulphuric acid. The bulk of the sulphur existing in proteins is split off as cystine during hydrolysis, and furnishes the body with sulphur. Eighty per cent. of the amount ingested reappears in the urine combined with aromatic poisons, such as phenol, indol, etc., derived from the putrefactive decomposition of protein in the intestinal canal. The sulphuric acid formed from cystine is combined with these poisonous products, which are thus safely escorted out of the body.

Carbonates are found in several of the secretions of the body, notably in the urine of the horse, where they cause the most intense evolution of gas on the addition of an acid The carbonates in the system of the herbivora result from the carbonates of the food, and the oxidation of vegetable acids, malic, citric, tartaric, etc.

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* Pigeons, rabbits, guinea-pigs, dogs, cats, goats. See Edie and Simpson, *British Medical Journal*, June 17, 1911, p. 1421.

These enter the body as salts of sodium and potassium, and are oxidised, by which means the acid portion is converted into carbonic acid and water, while the bases are set free. These unite with the carbon dioxide of the blood or lymph, and form carbonates.

The Nitrogenous Bodies.

Proteins.—The term 'protein' is applied to a group of organic substances which form the essential bases of all animal and vegetable tissues, both fluid and solid. Chemically, they are characterised by the presence of nitrogen, together with carbon, hydrogen, oxygen, and sulphur. The proportion in which these elements are found is liable to variation. For example :

	Per Cent.
Carbon	51·5 to 54·5
Hydrogen	6·9 ,, 7·3
Oxygen	20·9 ,, 23·5
Nitrogen	15·2 ,, 17·0
Sulphur	0·3 ,, 2·0

The protein group is chemically of a highly complex character ; their constitution is unknown, for they have never been obtained in a sufficiently pure condition for analysis. The molecule is known to be large, probably containing not less than 700 atoms of carbon. Some of the proteins have been crystallised, but neither the crystals so obtained nor protein itself are capable of diffusion through an animal membrane.

There are three classes of organic radicles in the protein molecule : one is purely basic, another is acid, and a third possesses both acid and basic properties. To this latter belongs the important class of **amino acids.** The characteristic feature of the amino acids is their ability to unite with one another or other organic bodies, and so form larger molecules. The complexity of the protein molecule is due to the presence of amino acids. These play a part which has been aptly compared by Garrod to that played by atoms in simpler chemical molecules.

A simple amino acid contains one organic acid radicle derived from the *carboxyl group* (COOH), and one organic basic radicle from the *amidogen group* (NH_2). Amino acids containing one amidogen group are termed 'mon-amino acids.' Those possessing two such groups are termed 'di-amino acids.' There is generally only one acid group, but there may be more. Thus there are mono- and di-basic mon-amino acids. The formation of amino acids may be illustrated by an interesting one formed from the simple fatty acid acetic acid $CH_3.COOH$. If the CH_3 group loses one of its atoms of hydrogen and this is replaced by NH_2, a substance known as *glycine*, or the amido acid of acetic acid is formed, $CH_2.NH_2.COOH$. Glycine may then conjugate with benzoic acid to form hippuric acid, and with cholalic acid to form glycocholic acid.

All the fatty acids are capable of forming different mon-amino acids, and the following series are then produced :

Mono-basic mon-amino acids : *Glycine, Alanine, Serine, Valine, Leucine.*

A second group is formed from fatty acids containing two carboxyl groups, *i.e.*—**Di-basic mon-amino acids** : *Asparagin, Aspartic acid, Glutamic acid,* and others less important.

A third series of mon-amino acids is the *aromatic*. In these the acid is united to the benzene ring, giving rise to the formation of—**Aromatic amino acids**: *Phenyl-alanine*, *Tyrosine*, and *Tryptophane*. It is from tryptophane that the substances which give rise to the offensive odour of fæces, indole and skatole, are derived.

In the group of **di-amino acids,** in which two amidogen groups (NH_2) replace two hydrogen atoms in the fatty acid series, greater complexity occurs, for the substances may act the part of either acids or bases. In this way are formed—*Lysine, Arginine, Histidine, Ornithine, Creatine, and Cystine.* The three first contain six atoms of carbon, and are in consequence spoken of as the hexone bases.

In addition to the amino acids, the protein molecule yields *Pyrrolidine derivatives*, *Pyramidine bases*, and *Ammonia*.

All the above groups of bodies are potentially present in the protein molecule—not necessarily in every variety of protein, for in some, as will presently be shown, certain cleavage products, as they are termed, are characteristically absent. Within the body the cleavage of the protein molecule is brought about by enzymes and putrefaction; in the laboratory, enzymes, putrefaction and acids at high temperature are employed, and in this way, piece by piece, the complex structure is taken apart. Within the body the reconstitution of the cleavage products into protein is rapidly effected; but in the laboratory attempts to reconstruct it have not yet been successful, though the question has engaged the attention of chemists for many years. Some portion of the structure has been erected, and substances giving protein reactions have been constructed by synthesis; but the chemist has not yet succeeded in making a typical protein.

The number of possible groupings of these end-products must be enormous. Even the simpler sugars containing six atoms of carbon present thirty-six possible combinations. The protein molecule contains not less than 700 atoms of carbon, and its variety of groupings is almost infinite. When the protein molecule is pulled to pieces, either in the laboratory or in the body, the process is effected by hydrolytic cleavage—*i.e.*, the protein takes up the elements of water and yields simpler substances. In the reconstruction of protein the chemical process is reversed, and dehydration employed. When proteins are pulled to pieces either within the body or in the laboratory, they yield *proteoses* (see p. 189) as the first cleavage product; these, in turn, furnish *peptones*. In the stage below peptones are groups of two, three, or more amino acids, termed *peptids* or *polypeptids*, and from these, as their connecting-links are broken, the individual amino acids are set free. Polypeptids are obviously much simpler chemically than protein, yet some notion of their complexity may be formed from the fact that a polypeptid has been prepared by synthesis with a molecular weight of 1213, and containing eighteen mon-amino acids, fifteen molecules of glycine, and three of leucine. The polypeptids in digestion are not numerous; the largest number are formed by synthesis.

Some proteins yield all the amino acids; in others certain of the acids are characteristically absent. For instance, gelatin does not contain either the tyrosine or tryptophane nucleus; serum-albumin, egg-albumin, the caseinogen of cow's milk, the protein of maize (zein), do not yield glycine, and the protein of wheat (gliadin) gives but traces. Leucine is abundant in serum-albumin, but much less in egg-albumin, and still less in gelatin. Glutamic acid is considerable in vegetable proteins, but relatively low in those of animal origin. The feeding value of a protein may be associated with the presence or absence of certain amino acids ; thus the absence of tyrosine and tryptophane from gelatin may explain why it is useless as food.

Classification of Proteins.—The following classification of proteins has been provisionally adopted :

Protamines.
Histones.
Albumins.
Globulins.
Sclero-proteins.

Phospho-proteins.
Conjugated proteins.
  (i.) *Chromo-proteins.*
  (ii.) *Gluco-proteins.*
  (iii.) *Nucleo-proteins.*
Derived Proteins.

Protamines.—These represent the simplest proteins known, and have been found in the spermatozoa of certain fishes.

Histones.—These bodies come next in order of complexity. They have been separated from blood-corpuscles, globin belonging to this group. Their specific chemical reaction is precipitation by ammonia.

Albumins. — This term is applied to the proteins found in tissue cells, serum-albumin, milk- and egg-albumin. It is characteristic of body proteins. Albumins are precipitated by saturation with ammonium sulphate ; they are not precipitated in *neutral* solutions by saturation with sodium chloride or magnesium sulphate, and are soluble in pure water. They are coagulated by heat in either neutral or acid solutions. Albumins yield no glycine on hydrolysis.

Globulins are found, together with serum-albumin, in body cells, blood, lymph, milk- and egg-albumin. They are precipitated by half saturation with ammonium sulphate, or by saturation with magnesium sulphate in neutral solutions, and in this way may be separated from the albumins. Globulins are insoluble in pure water, and yield glycine on hydrolysis.

Sclero-Proteins.—This is the modern term applied to a group of bodies originally described as *albuminoids*, of which *gelatin*, *elastin*, *chondrin*, and *keratin* are typical. These are found in bone, cartilage, tendon, horn, and hair. In the nervous system a substance is found similar to keratin, known as *neuro-keratin*. Its existence in nervous tissue is explained developmentally, for this system, together with the skin, hair, and hoofs, originates from the same layer in the embryo.

Phospho-Proteins.—These substances are distinguished by their richness in phosphorus, and the absence of purin bases on decomposition (p. 326). The latter feature distinguishes them from nucleo-proteins, which are also phosphorus-yielding, and with which they were originally confused. Phospho-protein is found in the yolk of eggs as *vitellin*, and in the casein of milk. This indicates their importance as food material in early life.

Conjugated Proteins.—These are proteins in which the molecule is united to other organic material, such as colouring matter, organic acid, or carbohydrate. *Chromo-protein* is protein united to a pigment — for example, hæmoglobin. *Nucleo-protein* (*chromatin*) is that united to an organic acid—nucleic acid—and found largely in the nuclei of cell tissue. It contains phosphorus, and the nuclein of the cells furnishes nucleic acid on decomposition. It is especially characterised by yielding certain purin bases on hydrolysis—viz., *xanthine*, *guanine*, *adenine*, and bases *of the pyramidine group*, which serves to distinguish it from the phospho-proteins. *Gluco-protein* is protein united with a carbohydrate group, of which mucin is typical. On decomposition mucin yields a reducing substance—*glucosamine*—which is not a true sugar.

Derived Proteins.—The hydrolysis of protein, as we have previously seen, yields a large number of end-products. But before this stage is reached, protein splits into intermediate bodies—*i.e.*, *meta-proteins*, *proteoses*, *peptones*, and *polypeptids*. *Meta-protein* represents the old acid and alkali albumins. *Proteoses* are of several varieties, *proto-*, *hetero-*, and *deutero-*, according to the stage of digestion. *Peptones* have previously been studied. *Proteoses* are precipitated by saturation with ammonium sulphate, but are not coagulated by heat. Peptones are not precipitated by ammonium sulphate. The *polypeptids* are formed as the result of digestive activity, but the majority are artificial products created in the laboratory during the reconstruction of the protein molecule.

The **Vegetable Proteins** constitute a large class, and group themselves under the same headings as the proteins of animal origin; but it is considered doubtful whether they are completely analogous. In the body they yield, during digestion, the same decomposition products as proteins of animal origin; but the end-products are not identical, glutamic acid being, as we have seen at p. 754, abundant in vegetable but low in animal protein; while the important tryptophane radicle is absent from maize. The solubility of vegetable is different from animal proteins. *Gliadin* (wheat and rye), *hordein* (barley), and *zein* (maize), are soluble in 70 to 80 per cent. alcohol, but insoluble in water or absolute alcohol. The term 'gliadins' has been proposed for the alcohol-soluble proteins of cereals. These are not found outside the cereal family. Other proteins found in cereals are readily dissolved by very dilute acids and alkalies. To these the term *glutelins* has been applied.

A very remarkable fact about protein substances is that, though they constitute the mainspring of organic life, yet they number amongst them, or amongst their decomposition products, some of the most powerful poisons known. Snake poison is a protein; even the albumose formed during the peptic digestion of albumin is highly poisonous if injected into the circulation.

Previous reference has been made to the fact that some proteins are capable of crystallisation. The crystallisation of hæmoglobin and some plant protein has long been known. Egg-albumin may also be crystallised, while serum-albumin of the horse is remarkable for the ease with which it may be obtained in a crystalline form (Fig. 260).

Tests for Proteins.—There are certain chemical tests which apply to the entire group of protein bodies, and others which are distinctive of members of the group. Their reactions are based on colour tests, precipitation, or coagulation.

Colour Tests—Xantho-protein Reaction.—Solutions of protein heated with strong nitric acid turn yellow, and on the addition of ammonia or caustic soda change to orange. This reaction is considered to be due to the presence in the molecule of some group of the aromatic series.

Millon's Reaction.—Millon's reagent is a mixture of mercurous and mercuric nitrates in the presence of nitric acid. When boiled with a protein solution, the mixture turns red, and the same colour is imparted to a precipitate should it occur. This reaction is supposed to be due to the presence of tyrosine in the molecular grouping, and is therefore not given when this is absent.

Piotrowski's Reaction.—To the solution of protein an excess of strong solution of caustic soda is added, and one or two drops of a 1 per cent. solution of copper sulphate. A purple colour results in the presence of protein, and a rose-red colour in the presence of proteoses and peptone. The essential feature is that the colour must be a purple, either red or blue. When protein in any form is absent, the solution remains blue. The term *biuret* is applied to this test, as a similar reaction is given with biuret, which is formed by heating urea.

Adamkiewicz's Reaction.—A mixture of one volume of concentrated sulphuric acid and two volumes of glacial acetic acid, when added to a solution of protein, produces a reddish-violet colour and slight fluorescence. The reaction is due to the presence of tryptophane in the molecule.

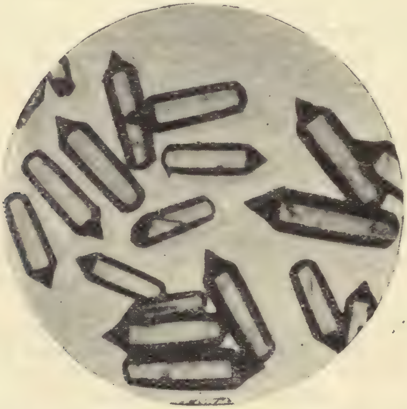

FIG. 260.—ALBUMIN CRYSTALS FROM HORSE-SERUM (GÜRBER).

The *precipitation* of proteins is brought about on the addition of mineral acids, such as nitric; salts of the heavy metals—for instance, acetate of lead or mercuric chloride—and by boiling; also by excess of alcohol; neutral salts of the alkalies—*i.e.*, sodium chloride and ammonium sulphate—to the point of saturation, and in many other ways. Halliburton draws attention to the necessity for distinguishing between coagulation and precipitation. For instance, a protein, on heating or on adding nitric acid, is coagulated; the precipitate is insoluble, but precipitates obtained by the addition of such substances as ammonium sulphate are soluble, and can readily be sent back into solution. To these the term 'precipitate' especially applies. The circumstances under which such precipitates are obtained have been mentioned under the head of Albumins and Globulins.

The Non-Nitrogenous Bodies.

Fats.—The fats found in body-fat, milk, and the marrow of bones, are compounds formed by the union of fatty acids with glycerine. These fats are *palmitin*, *stearin*, and *olein*.

Fatty acids are formed by the oxidation of alcohols, the group being a large one. Some of the earlier members of the series, such as acetic, propionic, valeric, caproic, have been referred to in speaking of the amino acids, for these form glycine, alanine, valine, and leucine, in the manner already described. The acids responsible for the body fats—palmitic and stearic acids—are the sixteenth and eighteenth in the *acetic* series, while oleic is the eighteenth in the *acrylic* series. A certain proportion of the fats in milk, and hence in butter, is formed from acids lower down in the acetic series, such as *caproic*, *caprylic*, and *capric acids*.

Fat is insoluble in water, and only slightly so in alcohol, but freely soluble in ether, chloroform, and benzene. When pure, it is neutral in reaction, tasteless and colourless, and by the action of caustic alkalies or superheated steam may be decomposed into its respective fatty acid and glycerine. When this splitting is brought about by an alkali, the base, sodium or potassium, at once unites with the free fatty acid and forms a salt (soap). This decomposition and saponification takes place to a greater or less extent in the intestine under the influence of the pancreatic juice and bile.

The solid fat of the body is composed principally of stearin, such as is found in the ox and sheep. The more liquid fat, such as is found in the horse and carnivora, contains palmitin, but in all cases a mixture of the three fats is obtained. Fat as it exists in the cells of the living body is, of course, in a liquid condition. Since the melting-point of palmitin is 45° C., and that of stearin 55° to 60° C., it is evident that the fluidity of living fat is due to the olein it contains, the melting-point of which is $-5°$ C. The amount of fat in the body must depend upon the feeding of the animal, and will obviously vary within extreme limits. In individual tissues marrow has the largest amount ; nerve, brain, milk, muscle, liver, bone, bile, and blood, have proportions which decrease in the order given. The change which the fats undergo in the alimentary canal has been discussed in the chapter on the Pancreas (p. 256), while the origin of fat in the body, and its function is dealt with under Nutrition (p. 358).

Lipoids.—This term is applied to a group of bodies found mixed with fat in various tissues and organs of the body, especially with protoplasm, cellular structures, and nervous tissue. The groups are distinguished by their chemical composition. One important member (*cholesterin*) contains neither nitrogen nor phosphorus ; another contains nitrogen, but no phosphorus ; a third both nitrogen and phosphorus. The three to be considered are lecithin, cholesterin, and a group known as *galactosides*. **Lecithin** is a wax-like body consisting of glycerine, stearic acid, phosphoric acid, and a nitrogenous base known as *choline*. It occurs abundantly in the white matter of the nervous system, and is also found in cellular structures and in bile. In the latter some of it is united to a carbohydrate residue, and forms *Jecorin*. The function of lecithin in the system is unknown, but its wide distribution in cellular structures points to its being concerned in the processes of metabolism. The base choline mentioned above is poisonous, and on oxidation with nitric acid yields the extremely poisonous substance *muscarine*. Lecithin enters the body by means of the food, and the poisonous action of choline is probably prevented by the substances being broken up by the bacteria of the intestines into carbonic acid, marsh gas, and ammonia. It has been supposed that the presence of lecithin in the blood cells may prevent the escape of hæmoglobin. Halliburton suggests that corpuscular destruction may result from the products of the fermentative decomposition of lecithin. **Cholesterin** contains neither nitrogen nor phosphorus, and in this respect resembles fat. It is an alcohol, and the only one which occurs in the body in a free state. It is widely distributed in the tissues and cells, in the white substance of the nervous system, and in the liver, where it forms the main constituent of gall-stones. In the brain it may occur in a free state, and is recognised by the silvery fish-scale-like deposits in the pia mater of the cerebellum and the choroid plexus of the horse, where it not infrequently gives rise to growths in the lateral ventricles. In the bile it is kept in solution by the bile acids. Observations on the hæmolytic action of cobra venom suggest that cholesterin may assist in retarding cell dissolution. In the wool-fat of sheep and in sebum a form of cholesterin, known as *iso-cholesterin*, exists, which replaces the glycerine constituent of fat. Iso-cholesterin is found in lanoline (see pp. 311, 312), but is not identical with cholesterin, as it does not yield Salkowski's test (see below), and turns the plane of polarised light to the left instead of to the right. Cholesterin is found in some plants, and it has been shown that animal cholesterin belongs chemically to the terpene series, which hitherto has been considered as exclusively connected with vegetable substances. It has been common to regard cholesterin as a waste product in the body, but it is likely, from what has been said above, that this view may require to be modified. That some of it is excreted is undoubted, for it is found in the fæces, but by then it has probably performed its functions. Cholesterin is readily soluble in cold acetone, ether, chloroform, and bile salts. It is insoluble in water and cold alcohol. It can easily be obtained in characteristic crystals. The two chief tests for its presence are performed by dissolving the substance in chloroform, and acting on it with sulphuric acid. If its solution in chloroform be shaken with an equal volume of strong sulphuric acid, the solution turns red, then purple, and passes through blue and green to yellow (Salkowski's test) ; or if sulphuric acid be added drop by drop to the solution of cholesterin in chloroform, a red colour turning to bluish-green results (Liebermann's test). **Galactosides** contain phosphorus, but no nitrogen ; they can be extracted from the brain, but little is known regarding them or their function. They yield on decomposition a reducing sugar known as *galactose*.

Carbohydrates.—This important class is of the greatest interest to the physiologist, inasmuch as the bulk of material consumed as food, especially in the herbivora, consists of carbohydrate matter. It is an extensive group of bodies consisting of such substances as starch and its derivatives, the various forms of sugar, and cellulose. Though so much carbohydrate material enters the body, but little can be found in the tissues. An animal starch (glycogen) is found in the liver and other organs, minute amounts of sugar are found in the blood, and a sugar exists in milk ; but very much less carbohydrate is recoverable from the body than enters it as food, for the reason that the bulk of it becomes converted into fat, or is rapidly oxidised to carbonic acid and water as a source of heat and energy to the body.

The carbohydrates may be divided into the

Starch group, or *polysaccharides.*
Cane-sugar group, or *disaccharides.*
Dextrose group, or *monosaccharides.*

Polysaccharides—*Starch.*—The formula for starch is unknown; it is considered to be $(C_6H_{10}O_5)n$, where n is not less than 5 or 6, and is probably very much larger. The molecular weight is also unknown.

Starch exists in plants in the form of grains, the shape of which depends upon the group from which they are derived; thus potato, bean, wheat, and other starch grains, have each a distinctive shape. The grain is composed of two parts, an envelope known as *cellulose,* and an interior called *granulose.* The granulose is the true starch; the cellulose is not, however, identical with the ordinary cellulose of plants. Starch is insoluble in cold water, but when boiled the grains burst, and a viscid, opaque, pasty mass results, which is not, however, a true solution of starch. A solution of starch can be obtained from this mass by *careful and limited* digestion with an enzyme, such, for instance, as human saliva, or by the action of dilute acid; when this takes place the material becomes watery, perfectly transparent, and filters readily, while previously this was impossible. To this limpid fluid the name 'soluble starch' has been given. The characteristic test for starch is the blue colour produced on the addition of iodine. Starch has no reducing action on Fehling's solution.

Dextrin.—When starch paste is acted upon by dilute mineral acid, or the enzymes found in the saliva and pancreatic juice, soluble starch is first formed as above described; but if the process be allowed to continue, further changes rapidly occur, leading to the production of dextrin and finally of sugar. There are probably several dextrins, though two are generally more particularly described—viz., *erythro-dextrin* and *achroo-dextrin.* These are distinguished from starch and from each other by their colour reactions with iodine, erythro-dextrin giving a reddish colour, while achroo-dextrin gives no colour. Much the same change which can thus be brought about by acting upon starch out of the body takes place in a more perfect and complete form within the body. The conversion of starch into dextrin and finally into sugar under the influence of certain enzymes performs a most important physiological function; neither starch nor dextrin is capable of being absorbed as such, whereas the sugar which results from this conversion is readily assimilable.

Glycogen closely resembles starch. It is found in several of the tissues of the body, and its origin and use have been previously discussed (see p. 247). It may be obtained as an amorphous white powder, readily soluble in water, and gives with iodine a port-wine colour instead of blue. By the action of acids or enzymes it is readily converted into dextrin, and finally into sugar. The sugar resulting from the action of acid is dextrose, whereas that produced by the enzyme is maltose; in the liver the sugar produced is dextrose and not maltose, and the method by which this conversion is obtained has been previously dealt with.

Cellulose, though not found in the animal body, is of great interest to the physiologist from its intimate relation to the feeding of the herbivora. The food substance in plants is locked up in a cellulose envelope, and until this envelope is broken down the material within cannot be acted upon by the digestive juices. This breaking down is accomplished by laceration during the process of mastication, but also by a subsequent digestion of the covering, by which means it is removed and the food substance exposed. The digestion of cellulose is a physiological puzzle. for the reason that no vertebrate is known to secrete a cellulose-dissolving enzyme. In certain invertebrates a true cellulose enzyme (*cytase*) is met with, and is known to be secreted in the intestinal canal. Inasmuch as the herbivora are capable of dealing with cellulose, the question of its solution is of the greatest interest. Bunge has shown that sheep can digest from 30 to 40 per cent. of the cellulose of sawdust and paper when mixed with hay. There is every reason to think that all the herbivora deal quite as thoroughly with the cellulose naturally found in their food. The question has been before us in dealing with Digestion (p. 193), in which it was shown that in the case of oats the grain provided its own cellulose-dissolving ferment. It is hardly likely that the sawdust or paper in Bunge's experiment provided their own enzyme, so that it is probable the hay furnished it. Cellulose, however, may be digested by the action of putrefactive organisms, either outside or inside the body. In both cases it is attended by the formation of acetic and butyric acids, and the evolution of marsh gas, carbon dioxide, and other substances. We have previously studied the facilities which exist within the body for the necessarily slow maceration of cellulose, which is the essential prelude to its solution (see pp. 195, 216, 220).

Disaccharides ($C_{12}H_{22}O_{11}$).—**Saccharose,** or cane-sugar, is not found as part of the animal body, but exists largely in plants, and forms a well-known supply of carbohydrate to the system. Cane-sugar does not give some of the characteristic sugar reactions; among others, it has no reducing action upon salts of copper, but by boiling with dilute mineral acids it is converted into equal parts of dextrose and lævulose, and the same change may be effected by enzymes in the stomach and small intestines. This conversion of cane-sugar is recognised by the changed action of the solution on polarised light, the rotation of the plane of polarisation being now left-handed instead of right-handed, as it was previously to the conversion; that is to say, it is *inverted*, hence the name *invert sugar*. If cane-sugar be injected into the circulation, it passes out of the system unaltered. Before this sugar can be assimilated, it must be converted into dextrose (see p. 248).

Maltose is formed by the action of malt extract (diastase) on starch paste, also by the action of saliva and pancreatic juice upon starch paste and glycogen. In its reactions it corresponds closely to dextrose, but it has a one-third less reducing action upon Fehling's solution, and, unlike it, does not reduce Barfoed's reagent.* Its specific activity in rotating the plane of polarised light is considerably greater than that of dextrose, being about $+140°$, as against $+52°$ for dextrose. Maltose yields an osazone when heated with phenylhydrazine hydrochloride. When heated the crystals (phenyl-maltosazone) melt at 206° C., and this, together with the shape of the crystals and their specific solubility in 75 parts of boiling water, renders the identification of maltose easy. Maltose, like cane-sugar, is non-assimilable, for if injected into the circulation it is excreted unchanged. Before absorption it has to be converted into dextrose, and this is effected by a ferment, *maltase* (p. 256).

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* A solution of cupric acetate to which acetic acid is added.

Lactose, or milk-sugar, is found solely in milk. It reduces Fehling's solution, and has the same rotatory power as dextrose, but it does not reduce Barfoed's reagent, nor does it undergo direct alcoholic fermentation with yeast. If boiled with dilute mineral acids, it is converted into equal parts of dextrose and galactose. Lactose readily undergoes lactic fermentation, as, for instance, in souring milk. The cause of this is a micro-organism ; but there are reasons for believing that an enzyme may also bring it about. In spite of the fact that isolated lactose is unable to ferment in the presence of yeast, yet an alcoholic fermentation is capable of occurring in milk, such, for instance, as in the *koumiss* from mare's milk and *kephir* from cow's milk. It is probable that the changes which bring this about are very complex, and due to several organisms.

Lactose, like saccharose and maltose, is non-assimilable as such, and it is probable that it is changed into dextrose before absorption, not necessarily as the result of the action of any digestive secretion, but during its passage through the intestinal wall. Like maltose, lactose yields an osazone, phenyl-lactosazone, which crystallises in characteristic rounded clumps of yellow crystals. These crystals melt at 200° C., and are soluble in 80 to 90 parts of boiling water.

Monosaccharides ($C_6H_{12}O_6$).—When the members of the preceding group of sugars, the disaccharides, are boiled with dilute acids or otherwise hydrolysed, they take up a molecule of water and split into two molecules of a new sugar. Thus cane-sugar yields dextrose and lævulose, maltose gives two molecules of dextrose, and lactose yields dextrose and galactose. Of these the most important is—

Dextrose, Glucose, or **Grape-Sugar.**—This is probably the form to which all sugars must be reduced in the alimentary canal, whether before or during absorption, in order that they may be assimilable by the tissues. In its ordinary reactions dextrose resembles maltose, but may be easily distinguished from it by the following differences in behaviour. Its specific rotatory power is only $+52°$. It reduces Barfoed's reagent (see Maltose). The osazone it forms, phenyl-glucosazone, crystallises in fine yellow needles ; these melt at 205° C., and, unlike the corresponding compound of maltose, are almost insoluble in water. Dextrose is capable of undergoing three fermentations—*i.e.*, alcoholic, lactic, and butyric ; the latter two are probably always present in the intestinal canals of animals, especially after a carbohydrate diet. Dextrose is found in the blood and many organs of the body. It is also the form in which sugar escapes by the kidneys in diabetes.

Lævulose.—This occurs in fruits and honey, mixed with glucose ; It may also be prepared by acting upon cane-sugar with sulphuric acid, by which means the cane-sugar is converted into equal parts of dextrose and lævulose.

Inosite.—This is a crystallisable substance, found among the 'extractives' of many tissues, usually in very minute quantities, though it is markedly present in heart-muscle and in the muscles of the horse, which may contain as much as 0·003 per cent. It occurs also in semen. Inosite is found abundantly in vegetable tissues, especially in unripe beans, which thus provide a convenient source for its preparation. Possessed of a sweet taste, and as being originally found in muscles, inosite has at times been called 'muscle sugar.' But although its empirical formula is the same as that of a monosaccharide, it is not a sugar : its solutions exert no rotatory power on polarised light, they do not reduce metallic salts, form no osazone with phenyl-hydrazine, nor are they capable of undergoing alcoholic fermentation. It is, in fact, a member of the benzene series, and consists of a closed ring of six CH.OH groups.

The sugars of chief physiological importance are the **hexoses**—that is to say, a sugar such as dextrose which contains 6 atoms of carbon in the molecule, or the disaccharides, which contain 12. A series of artificial sugars have been produced containing 3 (trioses), 4, 5 (pentoses), 7, 8, and 9 atoms of carbon in their molecule. Of these the pentoses alone at present possess any physiological interest. This is due to the fact that a *pentose* may be obtained by the decomposition of the nucleo-proteins of the pancreas and of yeast cells These pentoses are not assimilable, as shown by their rapid appearance in the urine after introduction into the body. Pentose yields an osazone which melts at 160° C.

Tests for Sugar—1. *Trommer's.*—An excess of caustic potash and a small amount of dilute solution of copper sulphate is added to the fluid and the whole heated. The copper is reduced to suboxide by the sugar, and a red precipitate falls. Fehling's solution, which is used as a *quantitative* test for sugar, consists of hydrated cupric oxide in caustic soda, and the double tartrate of sodium and potassium. The principle of this test is the same—viz., the reducing action of the sugar, which robs the cupric compound of its oxygen.

2. *Moore's.*—A solution of sugar boiled with caustic potash turns brown.

3. *Böttcher's.*—Bismuth oxide and excess of caustic potash are added to the fluid containing sugar and heated. The solution becomes grey and then black, from the deposition of metallic bismuth.

4. *Picric Acid Test.*—Boil the solution of sugar with a little picric acid and caustic soda in small quantities ; a brown-red opaque coloration is obtained.

5. *Fermentation Test.*—The fluid containing a piece of yeast is placed in a tube and inverted over mercury. If sugar is present it undergoes fermentation, and carbonic acid is given off, which collects in the tube.

The osazone tests have already been described under the respective sugars. They are very important to chemists for the discrimination of the various sugars, as well as for their identification.

The Ferments.

The conversion of one substance into another by the process of fermentation must have acted as a stimulus in the search for the philosopher's stone. To the ordinary mind, if sugar could be converted into alcohol, why not lead into gold ? The extraordinary phenomenon of a body being wholly changed into another, and bearing not the faintest resemblance to its progenitor, is not only one of the astonishing facts recorded by chemistry, but one of the wonders of science. The name ' fermentation ' was applied to the oldest example of this phenomenon, and indicated a restlessness or agitation in the fluid, the outcome of the generation of gas. When, later on, this was shown to be due to the activity of micro-organisms, these latter were naturally described as **ferments.** This term has remained, though fermentation is now known not to be exclusively produced by living organisms, but that non-living material may also excite it. To these non-living ferments the distinguishing name of **enzymes** is applied.

Very little is known of the process of fermentation. The first important addition to a knowledge of the subject was the discovery of the above fact, that a ferment may be either living or non-living matter—or, as it is termed, *organised* and *unorganised*—and that no essential difference exists between them, as the living ferment acts by producing within itself an enzyme which does the work. It is by means of enzymes or ferments that all the striking phenomena connected with the processes of digestion are carried out. None of the food substances taken into the alimentary canal are capable of absorption excepting through their agency, so that the importance of a study of fermentation in this connection alone is of the greatest interest; the part played by ferments in the liver, in the clotting of blood and milk, and the formation of ammonia from urea, has been previously pointed out.

The explanation of fermentative processes is considered to be due to *catalysis*, or a reaction induced by the presence or contact of another substance, called a *catalyser*, which takes no part in the reaction. Such bodies are known in inorganic chemistry—for example, the union of oxygen and hydrogen at ordinary temperatures to form water is induced by the presence of spongy platinum, which in itself undergoes no change, but by its presence accelerates the rapidity with which the union occurs, or, as the chemist expresses it, the *velocity of reaction*. In organic chemistry a good example of catalytic action is furnished by the change induced in a solution of cane-sugar in water. Under ordinary circumstances this is very slowly converted into equal quantities of lævulose and dextrose, but the addition of a little mineral acid effects it in a few minutes. The action of the acid is to increase the velocity of reaction. It is reasonable to suppose that the enzymes of the body and ferments generally act like the catalysers: they effect profound changes in the bodies with which they come into contact, but undergo no change themselves; and it may further be added that a very small quantity is capable, under suitable conditions, of acting indefinitely.

In order, however, that a ferment may act indefinitely, it is necessary that the products of its activity be removed as formed, as they are in the intestinal canal by absorption. An accumulation of the products stops the reaction; but if these be removed, the process recommences. The arrest of fermentation by the accumulation of its own products is shown in some enzymes to be due to what is called a *reversible action*; the catalyser, in presence of the now excessive *mass* of the products of its own activity, effects a process of reconstruction into the original substances. This was first shown by the action of *maltase*—a ferment contained both in yeast and the intestinal juice—on maltose, which it converts into dextrose, though under suitable conditions it reconstructs a small quantity of maltose from dextrose. Similarly, as was pointed out at p. 256, the fats in the intestinal canal are acted upon by *lipase*, broken up, and rendered soluble. In the tissues lipase causes a reconstruction of fat. Under conditions where fat is lost to the body, it is lipase which splits it up and renders it capable of being oxidised as food.

The chemical action of nearly all body ferments is *hydrolytic*—*i.e.*, the substance acted upon takes up the elements of water, and splits into simpler bodies.

The activity of ferments is influenced by temperature. At freezing-point they are inactive for all ferments employed by warm-blooded animals. At 65° C. (149° F.) all body ferments are finally and irretrievably destroyed. The most favourable working temperatures for the ferments of the animal body are from 40° to 45° C. (104° F. to 113° F.). This fact is necessarily ascertained by observations outside the body. It is fair to assume that within the body the normal internal temperature of the animal is that which is most favourable to their activity. There are some ferments which act best in acid, others in alkaline media. Most enzymes of the body are soluble in water, glycerine, or in salt solutions. They may be precipitated from solution by an excess of alcohol, or in the case of the digestive ferments, by saturation with ammonium sulphate. It is doubtful whether any of the ferments have been obtained in a pure condition on precipitation. They adhere strongly to proteins, which are also thrown down by the above reagents. In fact, for long it was usual to regard the ferments as protein in nature, but belief in this view is shaken by the fact that some body ferments have been prepared which are apparently free from protein, though all contain nitrogen.

Some body ferments are secreted in an inactive form as a *proferment* or *zymogen* (p. 171), and stored up in the cell ready for use. They may be activated at the moment they are required, or the presence of another substance is necessary to activation. This may be of either organic or inorganic origin. In the former case the activating substance is spoken of as a *kinase*, of which the best example is that described at p. 254, in which *enterokinase* activates the trypsin of the pancreatic juice.

The specific action of ferments is a characteristic feature. No ferment can do the work of another. In the case of a secretion in which more than one ferment is present—as, for example, in the pancreatic juice—it is assumed that each of the characteristic fermentations of which it is capable—viz., fat-splitting, starch-converting, protein-splitting, and milk-curdling—are produced by separate enzymes. This characteristic is especially well marked in sugars, which, in their chemical nature, are closely related, yet each requires its own enzyme. For example, *lactase* will only act upon *lactose ;* it effects no change in *dextrose* or *maltose*.

The oxidations occurring in the tissues, the nature of which has always been a physiological puzzle, are brought about by ferment activity; through the agency of *oxidases*, already spoken of at p. 326. Such oxidases have been prepared from various tissues, and are found widely distributed in the animal body. It is supposed that the oxygen produced is obtained by the splitting off of oxygen from hydrogen peroxide. From liver, lung, muscle, and spleen, an oxidase has been obtained which is capable of oxidising hypoxanthin into xanthin, and xanthin into uric acid ; another animal oxidase is capable of oxidising aldehydes ; a third oxidises tyrosine ; while the oxidation of sugar can be effected by tissue juices or extracts of the various organs.

Frequent reference has been made throughout these pages to oxidations occurring in the tissues (see pp. 129, 130, 326, 365, 372, 408, 411), and the curious story of oxidation in muscle is related in detail at p. 358. The mind is liable to visualise these oxidations as if the body were a lamp. Such a temperature in the tissues would insure their destruction, while the carbon in the cells is not in the form of a wick charged with oil. The protoplasm is three-fourths water, and the problem presented in physiological oxidations is to understand the production of heat and energy by the oxidation of

ENZYME.	WHERE CHIEFLY FOUND.	ACTION.
Ferments acting on Carbohydrates.		
Ptyalin (salivary diastase).	Salivary secretion.	Converts starch to sugar (maltose).
Amylase (pancreatic diastase).	Pancreatic secretion.	Converts starch to sugar (maltose).
Liver diastase.	Liver.	Converts glycogen to dextrose.
Muscle diastase.	Muscles.	Converts glycogen to dextrose.
Invertase.	Small intestines.	Converts cane-sugar to dextrose and lævulose.
Maltase.	Small intestine, salivary and pancreatic secretion.	Converts maltose to dextrose.
Lactase.	Small intestine.	Converts lactose to dextrose and galactose.
Glycolytic (?).	Muscles (?).	Splits and oxidises dextrose.
Ferments acting on Fats.		
Lipase (steapsin).	Pancreatic secretion, fat, tissues, blood, etc.	Splits neutral fats to fatty acids and glycerine.
Ferments acting on Proteins.		
Pepsin.	Gastric juice.	Converts proteins to peptones and proteoses.
Trypsin.	Pancreatic juice.	Splits proteins into simple crystalline products.
Erepsin.	Small intestines.	Splits peptones into simpler products.
Group of autolytic enzymes.	Tissues generally.	Split proteins into nitrogenous bases and amino bodies.
Deamidising Enzymes.		
Nuclease.	Pancreas, spleen, thymus.	Splits nucleic acid, with formation of purin bases, etc.
Guanase.	Thymus, adrenals, pancreas.	Converts guanin to xanthin by splitting off an NH_2 group and ammonia (NH_3).
Adenase.	Spleen, pancreas, liver.	Converts adenine to hypoxanthin by splitting off an NH_2 group, as ammonia (NH_3).
Oxidases.	Lungs, liver, muscle, etc.	Cause oxidation of organic substances, as in the conversion of hypoxanthin to xanthin and xanthin to uric acid.
Catalase.	Many tissues.	Decomposes hydrogen peroxide.

a wet substance at the relatively low temperature of the body. The oxidations occurring in the living cell are now believed to be due to the agency of ferments, described above as oxidases. These are contained in the substance of the protoplasm. Oxidases are capable of regulating their own activity, instantaneously and enormously increasing oxidation, as during muscular contraction, or just as instantaneously reducing it to the working minimum when an excess is no longer required. Nor is the action of oxidases confined to utilising the free oxygen brought in by the blood. They can unlock oxygen from oxygen-yielding compounds, and there appears little doubt that it is in some such way that the carbohydrate material in muscle is burnt, and heat and movement produced.

The action of *autolytic enzymes* has been referred to at p. 372. These are found very generally distributed in the tissues.

A classification of the body ferments is not possible at present. In the table on p. 765, from Howell, those principally employed in digestion and nutrition are tabulated.

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